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Research Article

Successions of terrestrial invertebrate communities during the Tsey Glacier retreat, Central Caucasus

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Abstract

In the Caucasus, the total area taken up by glaciers is known to have reduced by 23% over the last 20 years. This natural experiment allows for additive and replacement models of autogenic succession of biocoenoses within paraglacial landscapes to be tested. A certain risk of the extinction of cryophilic species also exists. However, montane paraglacial successions of invertebrate assemblages have hitherto been studied neither in the Caucasus nor in Russia as a whole. Structural changes of taxocoenoses were traced in a spatial and temporal sequence of ten properly dated paraglacial sites in the Tsey Gorge, North Ossetia – Alania (1–170-years old) among the testate amoebae, earthworms, molluscs, myriapods, mites, spiders, harvestmen, pseudoscorpions, collembolans, and beetles. As the glacier retreats, in place of bare paraglacial wastelands, grassland communities are formed that, after 10–14 years, are replaced by shrub vegetation and, on 30–35-year old surfaces, by forest communities. Most of the invertebrate groups, once "appearing" along a postglacial transect, were recorded from most older plots as well. Yet, their taxocoenoses underwent considerable transformations through increasing (or an increase turning into some decline in beetles) the species diversity and a strong, often complete change in the taxonomic composition and dominance structure. The most considerable transformations were observed at all major vegetation changes. The "appearance" of some groups in the transect was determined not only by dispersion capacities but mainly by the environmental conditions of particular

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habitats. When comparing the composition of the pioneer postglacial species complex of the study region with that in the mountains of Europe's south and north, its high-degree regional specificity was noted, sometimes shown at the family level (in spiders). Spatial β-diversity of all larger taxa studied was mainly attributed to turnover (due to "the replacement model" of succession). The general level of change diminished towards the later succession stages. Endemic arthropod species were revealed both in pioneer grassland and developed forest communities.

Key words: chronosequence; climate warming; endemic; models of succession; pioneer species; species extinction

Introduction

As a response to the ongoing atmospheric warming, glaciers retreat in most regions of the world (Hock et al. 2019; Zemp et al. 2019; Ficetola et al. 2021; Marta et al. 2021). The "sterile" surfaces that emerge after the retreat of glaciers are quickly colonized by living organisms, and, over time, the structure of these new communities is changed during succession. Studying the mechanisms and rates of the formation of complex biocoenoses is important both for fundamental ecology and for analyzing the restoration capacities of ecosystems, especially in unstable climatic conditions.

Mountains, occupying about 10% of the Earth's land surface, are hotspots of global biodiversity, concentrating one-quarter of all terrestrial species on Earth with unique levels of endemism (Seijmonsbergen et al. 2018). Contemporary warming may lead to habitat fragmentation, extinctions, or upslope shifts of subnival species of animals and plants (Pizzolotto et al. 2014; Gibson-Reinemer et al. 2015; Cauvy-Fraunié and Dangles 2019; Gobbi et al. 2017, 2021; Gobbi 2020; Gobbi and Lencioni 2020; Harvey et al. 2023). In certain species of beetles and millipedes, the level of such displacement has already been established as 50–350 m per century (Moret et al. 2016; Gildado et al. 2021; Panza and Gobbi 2022), and the species composition of the mountain communities of a number of large taxa has changed over the past 160 years by an average of 12% per decade (Gibson-Reinemer et al. 2015). During some 30 years, the upper distribution limit of one moss mite species shifted almost one kilometer up (Fischer and Schatz 2013). Yet, a glacier retreat forms new potential habitats (refugia) for vulnerable high-elevation species, and studies on these postglacial community successions are therefore highly important (Gobbi 2020).

The gradual melting of glaciers since the Little Ice Age, that has been observed around the world, has led to the formation of a paraglacial series of differently aged sites that follow a similar trajectory at the decadal to hundred-year time scale (Matthews 1992). In such cases, when the duration of the study succession of vegetation and soil exceeds the lifespan of the scientist and his research, it is the chronosequence methodology that helps us understand community transformations, often being the single tool of research (Hodkinson et al. 2004; Walker et al. 2010). Although modern warming may itself "accelerate" succession, making it difficult to analyze the most recent data as a real chronosequence (Kaufmann 2002; Bråten et al. 2012).

The study of the dynamics of paraglacial invertebrate communities began in the Austrian Alps, where, already in the middle of the 20th century, the consisten-

cy of changes in phyto- and zoocoenoses was shown, and stages of the formation of invertebrate assemblages in the glacier forelands were identified (Janetschek 1949, 1958). However, modern studies with a more or less exact dating of the surface age have virtually started during this millennium only (Kaufmann 2001; Kaufmann et al. 2002; Hodkinson et al. 2004; Seniczak et al. 2006; Hågvar et al. 2009; etc.). The bulk of modern works on this topic have been carried out in the mountains of Northern and Southern Europe, with a well-deserved advantage in relation to ground beetles, spiders, oribatid mites, and springtails (see Hodkinson et al. 2004; Gobbi et al. 2006a,b, 2007, 2017; Hågvar et al. 2009, 2012, 2020; Hågvar 2010; Gereben-Krenn et al. 2011; Schlegel and Riesen 2011; Tampucci et al. 2015; Moret et al. 2016, 2020; Sint et al. 2018; Gobbi and Lencioni 2020; Valle et al. 2022; etc.). A large amount of data now allows for in-depth discussions about the origin and specificity of pioneer species complexes, the rate of succession, and the testing of potential models for these processes (Hågvar et al. 2020; Ficetola et al. 2021; Rosero et al. 2021; Hågvar and Gobbi 2022; Valle et al. 2022). Over the territory of Russia, postglacial successions of invertebrate communities following the Little Ice Age have never been studied. Only very recently did the first reports of springtails and insects found in cryoconites on the surface of glaciers appear (Mergelov et al. 2023).

In the Caucasus, the total area taken up by glaciers is known to have reduced by 23% for the period from 2000 to 2022 (Tielidze et al. 2022). As part of the project of the Russian Science Foundation "Following in footsteps of the Caucasian glaciers: the primary succession of arthropod assemblages," in the summer of 2021, we undertook mass collections of terrestrial invertebrates in the Central Caucasus at the foot of Tsey Glacier (Fig. 1).

The unique invertebrate fauna of the Caucasus, where the level of endemism in some groups reaches 30–70% (Dashdamirov and Schwaller 1992; Kryzhanovskij et al. 1995; Walther et al. 2014; Kokhia and Golovatch 2020) and many species have not been described yet, is perhaps not the best object for purely ecological research. Studies of zoocenoses formed during glacial retreats are often limited to relatively well-studied ground beetles (Gereben 1995; Gobbi et al. 2007; Brambilla and Gobbi, 2014; Moret et al. 2016, 2020; etc.) or, being multi-taxa investigations, are carried out at the level of larger taxa (Kaufmann et al. 2002; Rosero et al. 2021), due to severe problems in the identification of such vast groups as protists, nematodes, microarthropods, and rove beetles. Recently, research results on organism successions during glacial retreats using not only classical morphological tools but also environmental DNA metabarcoding have appeared (Raso et al. 2014; Sint et al. 2018; Rosero et al. 2021; Cantera et al. 2024; Guerrieri et al. 2023). The team of authors of the present paper consists mainly of zoological taxonomists, thus giving them a rare opportunity to fairly exactly assess the dynamics of taxocoenoses in a number of larger groups of animals that differ significantly in size, dispersion capacities, and lifestyle. Such a multi-taxa approach seems important for characterizing the succession of the animal population as a whole since it allows for the restoration capabilities of ecosystems to be assessed as objectively as possible.

Another significant problem hampering such research is the chronological linking of succession stages. In the absence of special data, researchers often use the distance to the edge of the glacier and/or the structure of the phytoco-

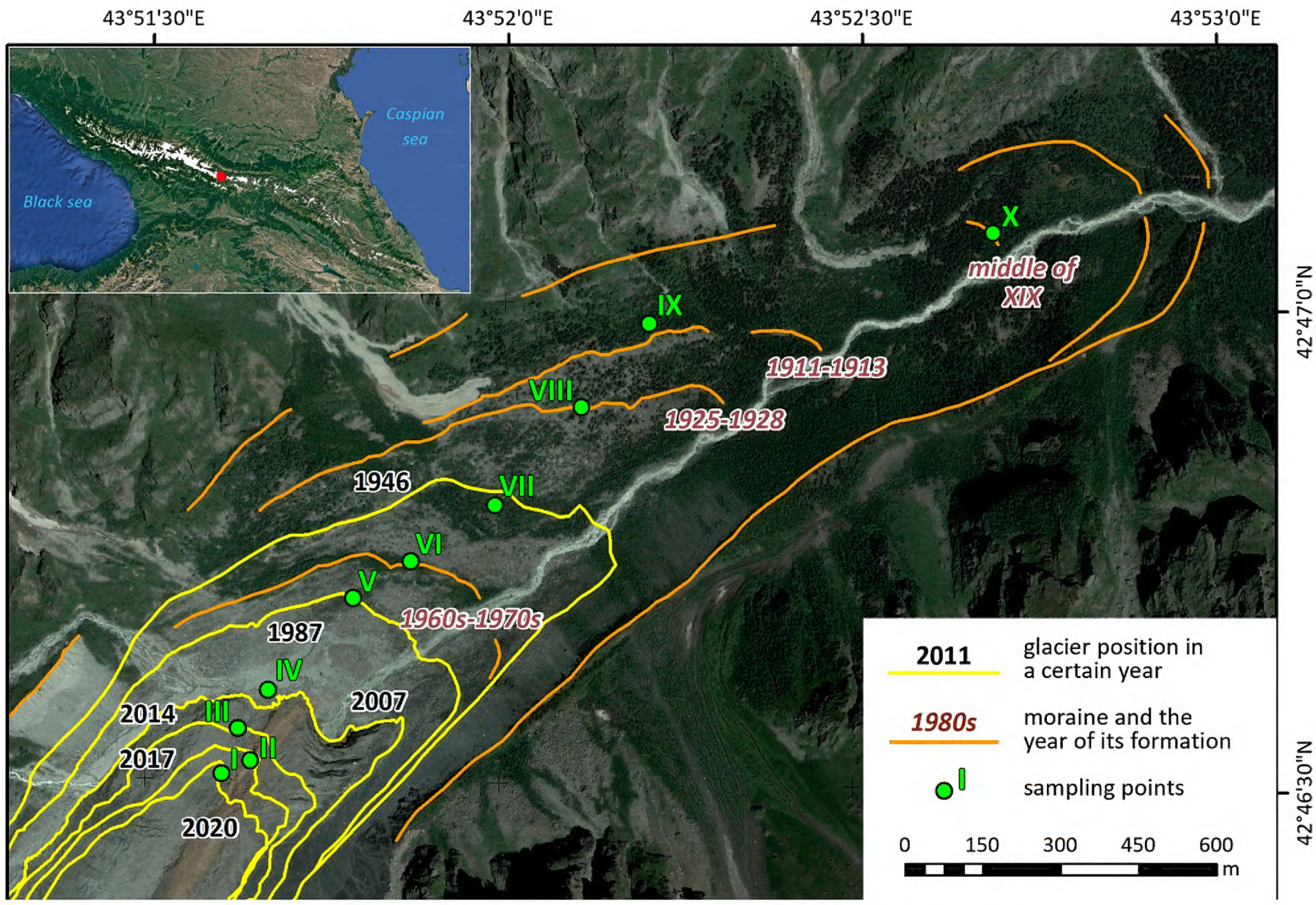


Figure 1. Location of the Tsey Glacier foreland, Adai-Khokh mountain massif, Central Caucasus.

enose as a measure of the community age (Schlegel and Riesen 2011; Lencioni and Gobbi 2018; Gwiazdowicz et al. 2020; etc.). This alone suggests possible errors in the case of glacier pulsation. To characterize the rate of retreat of the Tsey Glacier, a whole range of methods was used (Bushueva 2013), thus greatly facilitating the interpretation of zoological and ecological information.

In the recent study of invertebrates on an altitudinal profile in the highlands of South Tyrol, a significant restructuring of communities was shown, primarily due to an elevation itself with a higher species turnover rate at higher sites (Steinwandter and Seeber 2023). The bed of the Tsey Glacier has a relatively weak slope, and the vegetation of the study foreland profile is represented by grasslands as well as birch, pine, and mixed forests (Tables 1 and 2). The distribution of these forests in the Central Caucasus as a whole is often associated with areas of former glaciations (Grossheim 1936; Gulisashwili 1956). Given the significant extent of the study profile (1.8 km) with surfaces of various ages, the difference in elevation between sections I (1 year) and X (≈170 years) was only 265 m. Thus, we can assume that the observed differences between the natural communities along the profile are just due to the age of the surfaces, not the different altitudes above sea level.

The lack of information concerning the animal component of paraglacial successions (Matthews 1992), despite the rapid growth in the total number of publications in the last decade, is still topical because most of the research has focused on plants and microorganisms (Ficetola et al. 2021; Pothula and Adams 2022). Recently, in order to search for general patterns of succession,

papers have appeared that summarize data on several glaciers, including chronosequences from different continents (Vater and Matthews 2015; Sint et al. 2018; Cauvy-Fraunié and Dangles 2019; Hågvar et al. 2020; Hågvar and Gobbi 2022; Ficetola et al. 2021; Pothula and Adams 2022; Valle et al. 2022; Guerrieri et al. 2023; Cantera et al. 2024). Most researchers recognize that changes in natural communities during the colonization of ice-free surfaces are caused by a complex interaction between time factors, habitat transformation, and biotic interactions (Ficetola et al. 2021). The most important predictor of community structure is often considered to be its age (and therefore the timing of colonization), while the development of soil and vegetation (also associated with age) is interpreted as of secondary significance (Hodkinson et al. 2004; Gobbi et al. 2007; Schlegel and Riesen 2011; Guerrieri et al. 2023). Often, the degree of development of vegetation and soil (environmental filtering) is regarded as the most important predictor of zoological succession, naturally changing over time (Janetschek 1949; Kaufmann 2001; Kaufmann and Raffl 2002; Gobbi et al. 2006b, 2010, 2011). But some studies indicate a weak importance of vegetation as such (Hodkinson et al. 2001, 2002, 2004; Hågvar et al. 2009; Pothula and Adams 2022) and even the leading role of competitive relations in organizing the succession of individual groups, especially at later stages (Schlegel and Riesen 2011; Vater 2012; Ficetola et al. 2021). Since all these processes (colonization, environmental filtering, and interspecies competition) occur simultaneously, it has been repeatedly noted that analyzing their particular contributions to succession structuring is only possible in special experiments (Vater and Matthews 2015; Rosero et al. 2021).

Our study of the postglacial succession of invertebrates along the Tsey Gorge glacier foreland is the first to be performed in the Caucasus, and its main goal was to describe the temporal dynamics of the main larger taxa to create a framework for future, more analytical investigations. The participation of taxonomy specialists made it possible to do this quite accurately. For the first time, the rove beetles (Staphylinidae), the most diverse family of arthropods both along our profile and globally (Salnitska et al. 2022), were identified for a non-Scandinavian foreland collection. Thus, the objectives of our work were as follows:

1. to establish the timing of the appearance of the main groups of invertebrates along the dated chronosequence of Tsey Glacier's retreat;
2. to assess the rate of changes in the structure of individual taxocoenoses and the invertebrate fauna as a whole; and
3. to test succession models ("additive and persistence model" or "replacement model") using material from multispecies groups.

Materials and methods

Study area

The study area is located in a territory with the Terek Type of altitudinal zonation (Sokolov and Tembotov 1989), which is characterized by increased moisture and the predominance of broad-leaved, mainly beech, forests in the forest belt. The Tsey Glacier, one of the largest glaciers in the Central Caucasus (area

about 10 km^2), was formed in the Adai-Khokh mountain massive (height up to 4408 m) on the northern macroslope of the eastern part of the Greater Caucasus. The area of the upper reaches of the Tseydon River is composed mainly of crystalline rocks (granites, schists, gneisses, etc.). The climate of the Tsey Gorge is temperate continental, with a predominance of precipitation in the spring-summer period, but heavy snowfalls are most common in the second half of winter and early spring. The warmest month is July, and the coldest month is February, with average monthly temperatures at an altitude of 1750 m a.s.l., respectively, of 12.7 °C and −8.8 °C. The average annual precipitation at this altitude is about 800 mm (http://zapovednik15.ru). The main areas in the Tsey Gorge are occupied by beech, maple, birch, and pine forests. Above 2000–2500 m, forests are replaced by subalpine grasslands.

Choice of study sites

Various maps and remote sensing data have been used to assess the dynamics of the contours of the Tsey Glacier since the end of the 19th century. To determine the current position of the glacier, data obtained from Russian and foreign spacecraft were used. Images of the second half of the 20th century were taken from airplanes (aerial photography). One of the modern images was chosen as a reference, and all the others were linked to it. Image co-registration was carried out in two stages using the Erdas Imagine program (Hexagon). At the first stage, using control points and the digital terrain model STRM v3 (grid step 1 arcsecond), georeferencing was carried out using a second-order polygon. At the second stage, a new set of control points was collected, and image co-registration was refined using the "rubber sheet" method. The boundaries of the glacier were digitized manually. The map of military topographers of the late 19th century was fixed using a coordinate grid, and then this reference was refined using characteristic points of the relief. According to all these data, since the middle of the 19th century, the Tsey Glacier has retreated by approximately 1800 m, and only in the year preceding the collection of invertebrates (11.09.2020–23.06.2021) did it move back 16.0 m (North Ossetian Center for Hydrometeorology and Environmental Monitoring, request dated 07.07.2021).

On the transect (length about 1800 m) in the valley of the Tseydon River at the foot of the glacier, ten sample plots were marked with surface ages ranging from one to approximately 170 years (Fig. 1, Plots I–X). The selected sites included the main stages of primary vegetation succession (Figs 2–3): the almost bare ground, "grassland" and "shrub" stages, mixed, and finally mature pine (*Pinus sylvestris* ssp. *hamata*) forest (Tables 1, 3). The sites ranged in altitude from 2071 to 2336 m a.s.l.

For each sample plot, a brief geobotanical description was made, and the structure of the upper (0–5 cm) soil layer was generally characterized (Tables 2 and 3). In soil samples from which microarthropods were extracted, the relative humidity was determined by weighing the cores before and after drying (at room temperature until air dried). As everywhere in postglacial chronosequences (Hodkinson et al. 2004; Ingimarsdóttir et al. 2012; Pothula and Adams 2022), the diversity of vegetation and its projective cover gradually increased over time (Table 2), and the substrate moisture, litter thickness, and organic carbon content in the mineral horizon increased (Table 3).

Table 1. The study habitats across the glacier's retreat zones and sampling efforts (Tsey Gorge, Central Caucasus, 17–31 July 2021).

Plot #	Year of ice retreat	Habitat type	Coordinates	Altitude (m a.s.l.)	Number of pitfall traps per day	Number of soil samples*	Volume of sifted litter (l)
I	2020	Sandy-gravel surface without evident vegetation	N42.775098°, E43.860182°	2336	94	8/3	0
II	2017	Sandy-ground surface with single plantlets and moss patches on stones	N42.775335°, E43.860852°	2320	74	8/3	0
III	2014	Reedgrass meadow with draft willows on moraine	N42.775882°, N43.860545°	2318	142	10/3	10
IV	2007	Sparse shrub association: willow-birch growth and isolated young pines	N42.776554°, E43.861253°	2295	150	10/3	20
V	1987	Young mixed forest with luxuriant forbs	N42.778163°, E43.863217°	2249	150	10/3	30
VI	1960–70	Park-like tall-grass birch grove	N42.778815°, E43.864567°	2244	150	10/3	30
VII	1946	Dense two-storeyed small-leaved forest with rich forbs	N42.779795°, E43.866527°	2233	110	10/3	30
VIII	1921–25	Sparse pine wood with birch and rhododendron on moraine	N42.781522°, E43.868547°	2205	150	10/3	30
IX	1911–13	Mature small-leaved forest (birch, willows)	N42.782985°, E43.870103°	2193	150	10/3	30
X	≈1850	Old mossy pine forest with rhododendron, strawberry and blueberry	N42.784627°, E43.878177°	2071	150	10/3	30

* before line – "microarthropod" (Tullgren funnels) samples (5x5x5 cm), after line – "Testacea" samples (5x5x3 cm); both added by above-ground plant parts and litter layer.

Sampling

The collection of material was carried out on July 17–31, 2021 (Table 1). Surface-active arthropods were caught using pitfall traps (plastic cups with a volume of 200 ml and a diameter of 6.5 cm). The traps were set randomly 3–5 m apart in the most typical microhabitats from July 18–29. At each of the selected sites, 15 traps without a fixative (water only) were installed, which were checked every other day. The total amount of sampling effort approached 1470 pitfall days, since some of the traps in the youngest areas due to natural causes (ice failure, flooding) did not "work" at times. Large arthropods and molluscs were also caught by hand searching, and atmobiontic springtails were collected mainly using an aspirator. In plots with developed turf or litter (III–X), entomological sifting was used (10–30 liters of plant mass per plot). All invertebrates were fixed in 96% alcohol.

On each plot, soil samples (125 cm^3 of soil + litter) were taken randomly at the most typical sites in 8–10 replicates for subsequent microarthropod extraction in Tullgen funnels (Table 1). Samples for the rhizopod extraction (75 ml of soil + litter) were taken in three replicates, likewise in the most typical microhabitats. Both types of samples included the above-ground parts of plants (not higher than 5 cm). Samples were preserved in a cool, individually enveloped paper and plastic bag for two days and processed in the Moscow laboratories. Microarthropods were extracted into 96% alcohol using Tullgren funnels

Table 2. Vegetation of study paraglacial zones of different ages, Tsey Gorge, Central Caucasus (July 2021).

Plot #	Age of surface, years	Landscape position (ground slope)	Stoniness, %	Trees (or shrubs) of upper storey				Woody species of middle storey and (lower storey)		Lower vegetation storey		
				Main/ accessory species	Canopy density, %	Height, m	ø, cm	Species composition	Height, m	Dominant species of vascular plants	Mass moss species	
											On ground (cover, %)	On stones or wood
I	1	Bottom of gorge (1–2°)	100	–	–	–	–	–	–	*Chamerion* sp.	–	-
II	4	Bottom of gorge (1–2°)	95	–	–	–	–	–	–	*Chamerion* sp., *Ch. caucasicum*, *Senecio caucasicum*, *Poa glauca*, *Stellaria anagalloides*, *Tripleurospermum caucasicum*, *Saxifraga* sp., *S. mollis*	*Pohlia filum*, *Bryum caespiticium*, *Bryum* sp., *Dicranella* sp. (<1)	*Pohlia filum*, *Orthotrichum* sp., *Hymenoloma crispulum*, *Niphotrichum canescens*, *Schistidium* sp.
III	7	Top of moraine (5°)	80–90	–	–	–	–	– (*Salix* spp., *Pinus* s.v. *hamata*)	–	*Calamagrostis arundinacea*, *Trifolium canescens*, *Hedysarum caucasicum*, *Astragalus* sp., *Vicia cracca*, *Chamerion* sp., *Ch. caucasicum*, *Alchemilla* sp., *Tripleurospermum caucasicum*, *Saxifraga juniperifolia*	*Pohlia filum* (3)	-
IV	14	Foot of the slope between moraines (10°)	50	*Salix* spp. / *Betula raddeana*	40	0.7-1.5 1.5–2	1–2 2–4	– (*Pinus* s.v. *hamata*)	–	*Alchemilla* spp., *Heracleum* sp., *Potentilla sericea*, *Leontodon* sp., *Hedysarum caucasicum*, *Trifolium* spp., *Chamerion caucasicum*, *Saxifraga cartilaginea*, *Papaver oreophilum*, *Gallium* sp., *Euphrasia* sp., *Taraxacum* sp.	*Niphotrichum canescens* (30)	-
V	34	Foot of the slope (5–10°)	20	*Pinus* s.v. *hamata* / *Betula* sp.	50	6–7 6–8	10-15 7-15	*Salix* spp.	1–4	*Alchemilla* spp., *Trifolium* spp., *Lamium* sp., *Chamerion caucasicum*, *Gallium* sp., *Calamagrostis arundinacea*, *Potentilla sericea*, *Hedysarum* sp., *Vicia cracca*, *Euphrasia* sp., *Leontodon* sp.	*Abietinella abietina*, *Brachythecium* sp., *Niphotrichum canescens*, *Niphotrichum elongatum* (15–20)	-

VI	51-61	Moraine between streams at the gorge bottom (5°)	5–10	*Betula* spp. / *Salix* spp.	90	8–10 6–7	15–20 10–18	– (*Juniperus communis depressa*, *Rubus idaeus*)	–	*Alchemilla* spp., *Epilobium* sp., *Chamerion caucasicum*, *Poa nemoralis*, *Agropyron* sp., *Luzula* sp., *Trifolium hybridum*, *Vicia cracca*, *Hedysarum* sp., *Heracleum* sp., *Crepis* sp., *Silene vulgaris*, *Taraxacum* sp., *Cicerbita racemosa*	*Sanionia uncinata*, *Plagiomnium cuspidatum*, *Entodon concinnus*, *Syntrichia ruralis*, *Brachythecium* sp. (3)	-
VII	75	Lower part of gorge slope (10–15°)	30–40	*Betula* spp. / *Salix* spp.	30–40	6–7 3–5	10–15 3–4	*Sorbus aucuparia* (*Pinus* s.v. *hamata*, *Juniperus communis depressa*, *Rubus idaeus*)	3–4	*Epilobium sp.*, *Betonica grandi*flora, *Calamagrostis arundinacea*, *Hedysarum* sp., *Rosa* sp., *Solidago caucasica*, *Trifolium caucasicum*, *Alchemilla* sp., *Vicia cracca*, *Lotus* sp.	*Sanionia uncinata*, *Lescuraea saxicola*, *Niphotrichum canescens*, *Schistidium* sp. (3)	-
VIII	96-100	Moraine in lower part of gorge slope (20°)	20–25	*Pinus* s. v. *hamata*	30	12–15	20–40	*Betula* sp. (*Rhododen*dron *caucasicum*, *Salix* spp., *Betula* sp., *Pinus* s.v. *hamata*)	6–10	*Calamagrostis arundinacea*, *Hedysarum* sp., *Solidago caucasica*, *Chamerion caucasicum*, *Crepis* sp., *Vaccinium vitis-idaea*	*Tortella tortuosa*, *Niphotrichum canescens* (5)	-
IX	108-110	Lower part of gorge slope (15°)	10–15	*Betula* sp. / *Salix* spp.	75–80	5–14 7–8	7–21 3–9	*Salix* spp., *Betula* sp., (*Pinus* s.v. *hamata*, *Juniperus communis depressa*, *Rubus idaeus*)	3–5	*Poa nemoralis*, *Poa* sp., *Trifolium canescens*, *T. hybridum*, *Geranium sylvaticum*, *G. renardii*, *Solidago virgaurea*, *Vicia cracca*, *Cichorium intybus*, *Vaccinium myrtillus*, *Heracleum* sp., *Lapsana intermedia*, *Companula* sp., *Pyrola media*, *Moneses uniflora*, *Silene vulgaris*, *Gymnocarpium dryopteris*	*Sanionia uncinata*, *Hylocomiastrum pyrenaicum*, *Niphotrichum* canescens, *Niphotrichum elongatum*, *Plagiomnium cuspidatum*, *Pseudoleskeella nervosa* (10–15)	*Orthotrichum* sp., *Grimmia elatior*, *Bryum moravicum*, *Schistidium* sp., *Sciurohypnum populeum*
X	≈170	Foot of the slope (5–10°)	20	*Pinus* s. v. *hamata*	50–60	15–20	35–40	*Betula* sp. (*Salix* spp., *Fagus orientalis*, *Betula* sp., *Pinus* s.v. *hamata*, *Rhododendron caucasicum*, *Juniperus communis depressa*, *Rubus idaeus*)	5–8	*Fragaria vesca*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Hedysarum* sp., *Trifolium caucasicum*, *Festuca* cf. *montana*, *Pyrola chlorantha*, *P. media*	*Sanionia uncinata*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomiadelphus triquetrus*, *Hylocomiastrum pyrenaicum*, *Niphotrichum elongatum* (30–40)	*Niphotrichum canescens*, *Dicranum* sp., *Hymenoloma crispulum*, *Schistidium* sp., *Grimmia* sp.

Table 3. Characteristics of soil "microarthropod" samples (litter + soil cube, 5x5x5 cm, replication 8–10) collected on the postglacial transect of the Tsey Gorge, Central Caucasus (July 2021).

Plot, #	Age of surface, years	Relative humidity, %	Litter (A_0)		Soil		
			Thickness, mm	Composition	Depth of humified layer, mm	Thickness of layer with visible thin roots, mm	Mechanical properties of ground and the humus type
I	1	8.05	0	–	0	5–10	Coarse grey sand among large rock debris
II	4	12.28	0	–	0	5–15	A mixture of small gravel (3–15 mm) and fine sand (yellow or grey)
III	7	16.32	0–3	Moss films	0–5	5–20	A mixture of gravel (15–20 mm) and medium and fine-grained grey sand; somewhere consolidated by moss films
IV	14	12.70	3–18	Grass and moss debris	0–13	5–20	Medium- to fine-grained grey sand, weakly cohesive
V	34	23.76	5–25	Grass and leaf litter, moss turf	6–40	20–25	Medium to fine grain sand (grey or yellow,), partially cohesive
VI	51–61	30.84	7–17	Grass and leaf litter, moss turf	>50	25–30	Mor + fine-grained sandy loam
VII	75	43.62	8–15	Grass and leaf litter	>50	25–35	Fine-grained yellow sand with single small (5–8 mm) pebbles
VIII	96–100	38.03	10–25	Leaf litter, pine needles, moss turf	30–50	30–40	Mor + mull + fine-grained yellow sand
IX	108–110	47.93	16–28	Leaf litter, moss turf	40–50	>50	Mor + mull + fine-grained yellow sand
X	≈170	36.73	20–35	Moss turf, pine needles, leaf litter	30–50	>50	Mor (moss debris) + mull + medium-grained yellow sand

by drying the samples (8–10 days) until their complete desiccation with neither additional heating nor lightening. Mites and collembolans were slide-mounted and identified mainly in Hoyer's and Gisin's mediums. Oribatid mites were partly mounted in lactic acid on temporary cavity slides. Soil samples for rhizopod analysis were prepared following a standard technique based on filtering and concentrating soil suspensions in water (Mazei and Chernyshov 2011). In order to count living individuals with cytoplasmic remains inside shells, the Bengal pink dye ($C_{20}H_4Cl_4I_4O_5$) was added to the concentrated suspensions.

Our survey did not involve special quantitative sampling of earthworms and molluscs. All of them were obtained by setting traps, taking soil samples, and intensive hand-catching. Many individuals were found in soil pitfalls.

Shrews (14 specimens), occasionally caught in soil traps, were also fixed in 96% alcohol and identified. Now they are kept in the Zoological Museum of the Lomonosov State University, Moscow.

Identification

Most of the mass groups of soil invertebrates were processed and considered, except for nematodes and dipteran larvae. All authors of this contribution are professional zoologists who have extensive experience in taxonomic research, thus making it possible to fully identify, and for the first time, thoroughly elucidate changes in species compositions along a postglacial transect. Indirectly, this also made it possible to assess the state of knowledge of individual inver-

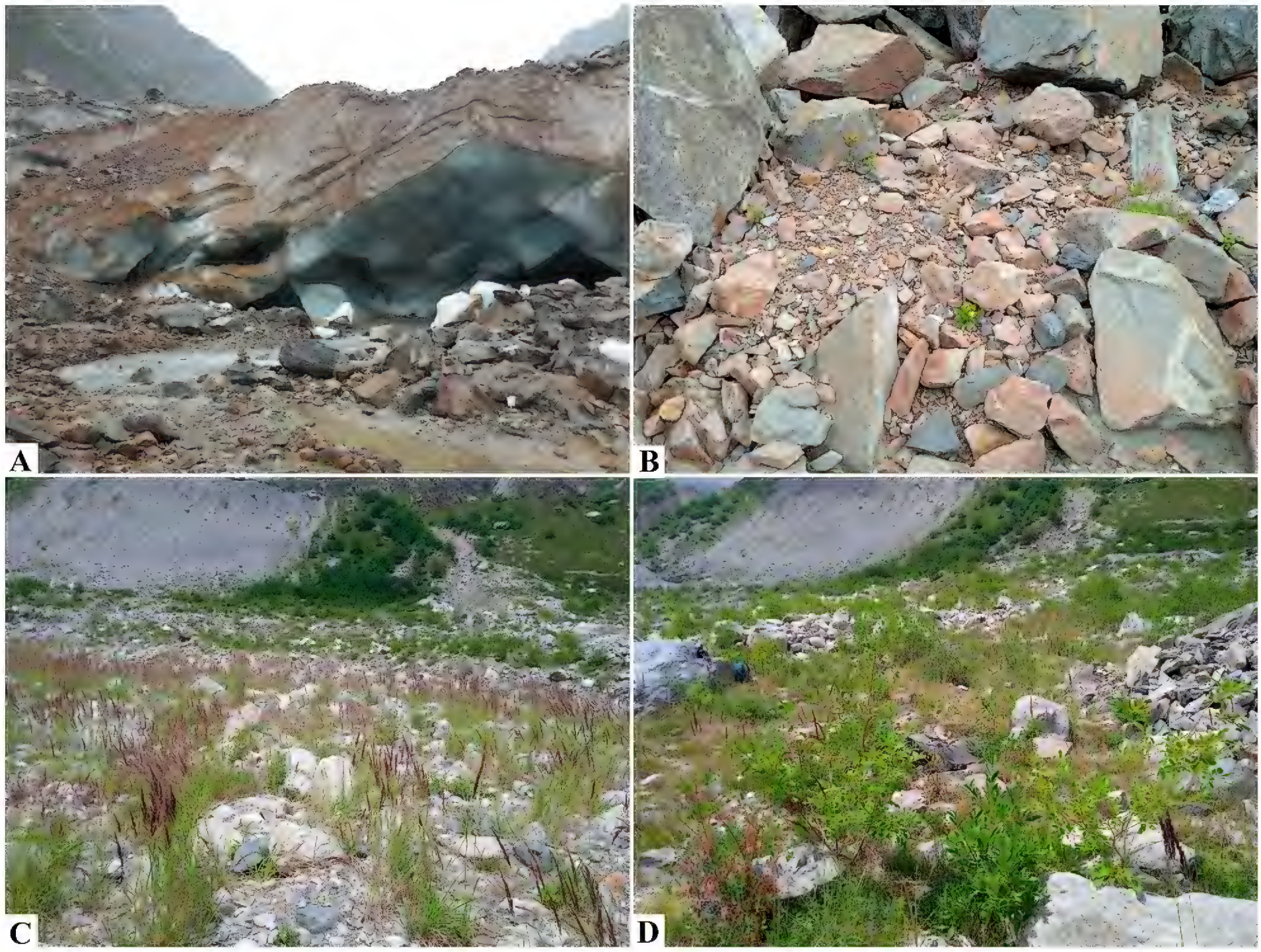


Figure 2. Sampling sites. **A**: Plot I (bare sandy ground, 1 year old after ice retreat); **B**: Plot II (sandy surface with single plantlets, 4 years old); **C**: Plot III (reedgrass meadow, 7 years old); **D**: Plot IV (shrub association, 14 years old).

tebrate groups in the Caucasus. The following is a list of the groups of animals indicating the specialists who determined the appropriate material: Testacea (A.D. Chulei, Yu.A. Mazei, A.N. Tsyganov), Lumbricidae (I.B. Rapoport), Mollusca (D.M. Palatov), Diplopoda (S.I. Golovatch), Chilopoda (R.V. Zuev), Acari, Mesostigmata (O.L. Makarova), Acari, Oribatida (V.B. Kolesnikov), Opiliones (N.Y. Snegovaya), Pseudoscorpiones (I.S. Turbanov), Araneae (A.V. Ponomarev), Collembola (A.B. Babenko, M.D. Antipova), Coleoptera, Staphylinidae (O.I. Semionenkov), Coleoptera, diversa (K.V. Makarov). Shrews were identified by B.I. Sheftel, mosses by G.Y. Doroshina, and vascular plants by K.P. Popov. All cartographic work was carried out by I.S. Bushueva. The invertebrates are kept in the corresponding authors' or museum collections.

Statistical procedures

Microsoft Excel 2010 was used for storing and primary data processing. We assessed the dynamics of changes in the composition of invertebrates along the foreland chronosequence employing the values of pairwise sample comparisons following Wilson and Shmida (1984), calculated using standard functions of Microsoft Excel 2010.

Figure 3. Sampling sites. **A**: plot V (young mixed forest, 34 years after ice retreat); **B**: plot VI (park-like birch grove, 51–61 years old); **C**: plot VII (dense small-leaved forest, 75 years old); **D**: plot VIII (sparse pine wood, 96–100 years old); **E**: plot IX (mature small-leaved forest, 108–110 years old); **F**: plot X (mossy pine forest with rhododendron, ~170 years old).

Calculations of α-diversity indices and the estimation of the expected number of species were carried out using PAST ver. 4.14 (Hammer et al. 2001).

The classification of communities has also been performed through the application of standard algorithms in PAST software. To test the assumption concerning the non-randomness (non-stochasticity) of succession, the presence

of large stages (phases) uniting particular successive stages (Plots I–X) was analyzed. For this purpose, three independent methods were used: non-metric multidimensional scaling, classical hierarchical cluster analysis, and flat analysis employing the K-medoids algorithm that is effective for assessing the ecological data (Kaufman and Rousseeuw 1990). In all cases, the Bray-Curtis similarity coefficient, commonly used for species abundance data, was applied (Magurran 2004).

To characterize the change of taxa in a series of postglacial communities, the Sørensen-based multiple-site dissimilarity index and comparisons of the contribution of the turnover (replacement) and nestedness (addition) components, proposed in Baselga (2010), were both utilized. Calculations were performed applying the betapart v.1.6 package (Baselga and Orme 2012) in the R v.4.3.2 environment (R Core Team 2023).

All charts were created using the Microsoft Excel 2010 facilities. Dominance classes followed Engelmann's (1978) classification.

Results

A total of 19,481 specimens of invertebrates belonging to 438 species were collected and identified, including 44 specimens of earthworms assigned to one species, *Dendrobaena octaedra* (Savigny, 1826), and 50 specimens of pseudoscorpions, *Neobisium* (*Neobisium*) cf. *vilcekii* Krumpál, 1983. Besides this, 17 specimens of shrews, including 15 *Sorex volnuchini* Ognev, 1921, and two *Sorex satunini* Ognev, 1922, were captured by pitfall trapping together with arthropods.

All specimens found of testate amoebae, molluscs, myriapods, harvestmen (except for two species represented by females only), pseudoscorpions, and beetles were identified to the species rank. Yet, 30 species could not be assigned to a certain taxon, apparently being new to science. These are 11 species of Mesostigmata (Acari), 10 Oribatida (Acari), 7 Collembola, and two species of Araneae.

Coleoptera, Oribatida, Mesostigmata, and Collembola showed the greatest species diversity (Table 4). The number of species of Araneae, live Testacea, and Gastropoda was 1.5–3 times lower, while Chilopoda and Opiliones were represented by only six species each. Despite the short-term collections, it was possible to identify most species of pedobionts. Depending on the assessment method (Table 4; Fig. 4), we revealed from 61–78% (Mesostigmata) to 91–98% (Testacea) of the expected number of species.

Almost all dominant species (>12.5%) of the pioneer stages (Plots I–III) are high-montane endemics of the Caucasus. On Plot I, such are the ground beetle, *Bembidion pulcherrimum* (Motschulsky, 1850), the springtail, *Desoria* aff. *duodecimoculata* (Denis, 1927), and the spider, *Pardosa* aff. *ibex* Buchar et Thaler, 1998; on Plot II, the rove beetle, *Geodromicus major* Motschulsky, 1860, the springtail, *Ceratophysella* aff. *succinea* (Gisin, 1949), and the mesostigmatic mite, *Lasioseius* sp.; on Plot III, the springtail, *Orchesella* aff. *caucasica* Stach, 1960, and the ground beetle, *Amara cordicollis* Ménétriés, 1832.

In the chronological series of habitats, significant rearrangements in the complex of invertebrates were revealed (Table 5). Some taxa almost immediately appear on the surfaces freed from ice (Fig. 2A, Plot I). Among them

Table 4. Number of sampled individuals, observed and expected numbers of species in multispecies groups (Tsey Gorge, Central Caucasus, 17–31 July 2021).

Taxon	Individuals	Observed species richness	Expected species richness				
			Chao-1	iChao-1	ACE	Squares	Mao tau's
Testacea (live)	792	27	27.6	28.4	29.1	28.4	29.7
Testacea (including numerous dead ones)	3801	46	47.5	50.8	47.1	46.8	51.2
Gastropoda	193	18	18.6	19.1	20.8	19.1	23.2
Oribatida	6174	68	73.6	76.9	74.6	84	85.9
Mesostigmata	1188	61	78.0	86.0	82.9	83.1	100.3
Opiliones	374	6	7.0	7.0	8.7	9.1	8.6
Araneae	324	39	47.6	52.0	54.9	73.8	52.0
Chilopoda	44	6	6.5	6.5	6.8	6.4	10.8
Collembola	6319	59*	65.0	67.3	65.7	68.1	78.3
Coleoptera	987	121	155.4	165.9	182	169.2	168.3

* – the number of Collembola species revealed totals 73, but 59 were the only ones statistically considered as coming from Tullgren funnels.

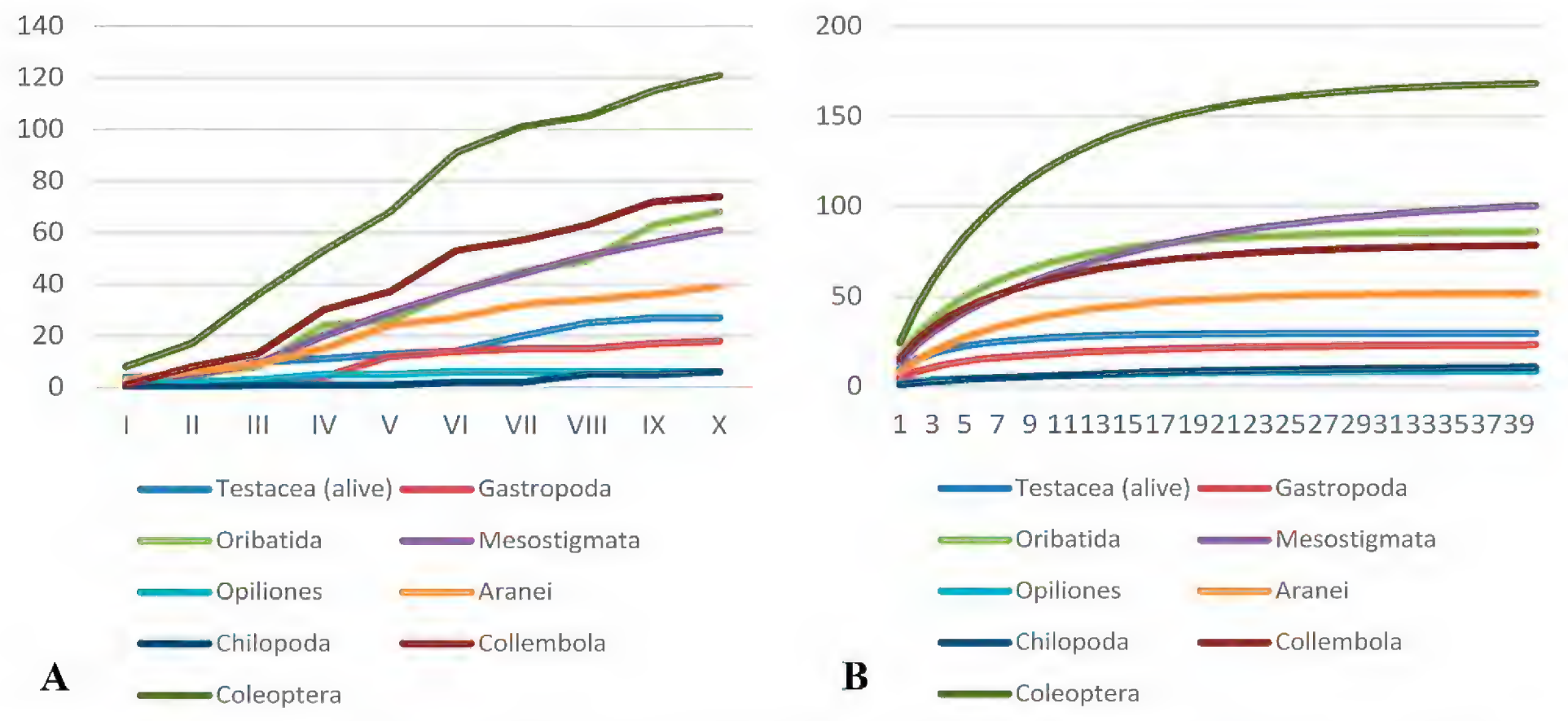


Figure 4. Species richness of pedobionts from the Tsey Glacier foreland. **A**: Observed cumulative species number (ordinate) from the sampling plots (abscissa); **B**: Expected species number (ordinate) as a function Mao's tau of the number of survey sites (abscissa).

are the testate amoebae, "flightless" microarthropods, spiders (ones that easily settle on arachnoid threads), wandering females of harvestmen, as well as well-flying predatory beetles (Carabidae, Staphylinidae) and bugs (Saldidae).

Sparsely vegetated, the 4-year-old Plot II (Fig. 2B) is already inhabited by enchytraeid worms, dipteran larvae of at least four families (including Chironomidae, Limoniidae, and Syrphidae), numerous aphids (up to 420 ind./dm^2), and thrips (up to 225 ind./dm^2).

On the 7-year-old Plot III with developed herbaceous vegetation (Fig. 2C), woodlice, soil molluscs, and predatory centipedes (Chilopoda) appear.

Table 5. Stages of the appearance of individual animal groups during the autogenic succession of communities formed after the Tsey Glacier's retreat (Central Caucasus, July 2021). In the table, combined data from sifting, Tullgren funnel extraction, pitfall trapping, and hand sorting is given

Taxon	Sequence number of plot and age of its surface (in parentheses), years									
	I (1)	II (4)	III (7)	IV (14)	V (34)	VI (51–61)	VII (75)	VIII (96–100)	IX (108–110)	X (≈170)
Testacea	+	+	+	+	+	+	+	+	+	+
Acari	+	+	+	+	+	+	+	+	+	+
Araneae	+	+	+	+	+	+	+	+	+	+
Opiliones	+	+	+	+	+	+	+	+	+	+
Collembola	+	+	+	+	+	+	+	+	+	+
Hemiptera	+	+	+	+	+	+	+	+	+	+
Thysanoptera	+	+	+	+	+	+	+	+	+	+
Coleoptera	+	+	+	+	+	+	+	+	+	+
Diptera, LL	+	+	+	+	+	+	+	+	+	+
Mollusca			+	+	+	+	+	+	+	+
Chilopoda			+	+		+		+	+	+
Isopoda			+	+	+	+	+		+	
Diplopoda				+			+	+	+	+
Lumbricidae				+	+	+	+	+	+	+
Insectivora				+	+		+		+	+
Siphonoptera				+	+	+	+	+		
Pseudoscorpiones						+	+	+	+	+
Blattoptera										+

On the 14-year-old Plot IV, with complex shrubby vegetation (Fig. 2D), the first earthworms and millipedes were found. Besides this, first shrews accompanied by their parasites (fleas, ixodids, and gamasid mites) were recorded in pitfall traps.

Later than the other groups, after 34–61 years (Plot VI), already in proper forest communities with a well-developed litter layer and a significant humus horizon (Fig. 3B), the first pseudoscorpions were reported. And only a century and a half later (Plot X, Fig. 3F), on the site of the former glacier, the first cockroaches (Ectobiidae) were discovered.

All main groups of invertebrates, once "appearing" on the postglacial transect, are also recorded in older stages. The α-diversity dynamics pattern of particular invertebrate groups on the study profile is strictly individual (Figs 5, 6). Endemic species are present in all stages. The species diversity of all multispecies taxa is generally increased during succession (the Shannon index value growing to 2.7–3.8), but beetles stand out by their high level of diversity. Starting with Plot IV, their Shannon index does not fall below 2.8, while for other taxa, its value fails to exceed 2.7.

In spite of a generally additive pattern of community change at the class-order taxonomic level (Table 5), individual taxocoenoses undergo significant restructuring since their species composition and the array of dominant species change radically, often completely. All groups, with the exception of the general pool of testate amoebae (dead and live specimens) only, demonstrate a significant species turnover whose intensity drops in the last stages of succession (Figs 6–8).

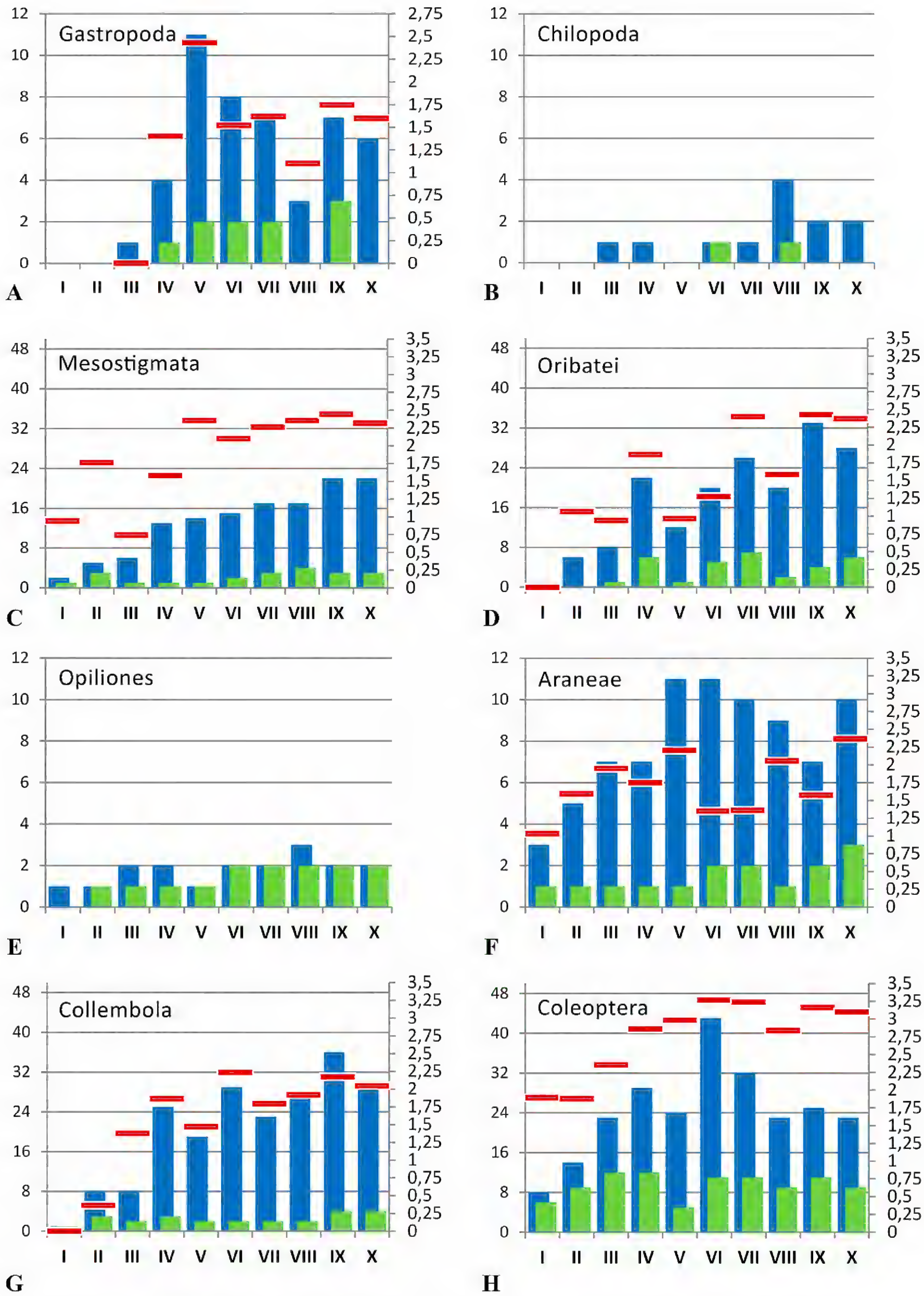


Figure 5. Total number of species (blue bars), the number of Caucasian endemics (green bars) and the value of Shannon index (red lines) on the study chronosequence. The left ordinate is for the number of species, the right one is for the Shannon index. **A**: Gastropoda; **B**: Chilopoda; **C**: Mesostigmata; **D**: Oribatei; **E**: Opiliones; **F**: Araneae; **G**: Collembola; **H**: Coleoptera.

Discussion

Review of taxonomical groups

Rhizopoda. In total, 46 species or subspecies of testate amoebae belonging to 21 genera and 14 families have been recorded from the habitats of the Tsey profile. All species have been identified and show vast distributions.

Testate amoebae have already been revealed in the sand on the surface of the Tsey Glacier (9 species found). As noted earlier (Carlson et al. 2010), they almost immediately colonize substrates just freed from ice. The species richness of taxocoenoses in areas without vegetation cover (Plots I, II) did not exceed 11 species, and the dominance structure was unstable (Fig. 6). Cosmopolitan hydrophilic species predominated (*Galeripora catinus* (Penard, 1890) González-Miguéns et al., 2021; *Centropyxis cassis* (Wallich, 1864) Deflandre, 1929; *Centropyxis elongata* (Penard, 1890) Thomas, 1959; *Centropyxis orbicularis* Deflandre, 1929; and *Centropyxis sylvatica* (Deflandre, 1929) Bonnet and Thomas, 1955), probably due to increased soil moisture at the ice edge. With the appearance of grassland vegetation (Plot III), the species richness increased (17 species), and the dominance structure stabilized with a predominance of typical soil (*C. sylvatica* and *Plagiopyxis declivis* Bonnet, 1955) and small eurybont (*Trinema lineare* Penard, 1890) species. The species *Centropyxis cassis* deserves special mention, being clearly confined to the pioneer stages (1–4 years in age) to disappear later. This species was mainly represented by live individuals, thus excluding its passive transfer from outside.

At the shrub stage (Plot IV), the species richness reached 22 species, this already being comparable with the diversity in later successional forests, with bryophilous species appearing (*Assulina muscorum* Greeff, 1888; *Centropyxis minuta* Deflandre, 1929; and *Heleopera petricola* Leidy, 1879). The forest stage (Plots V–X) is characterized by the highest species richness (on average about 30 species per sample), the array of dominants remaining relatively stable, and larger pedobiont species appearing (*Argynnia dentistoma* (Penard, 1890); *Centropyxis plagiostoma* Bonnet et Thomas, 1955; *Euglypha rotunda* (Ehrenberg, 1845); *Euglypha simplex* Decloitre, 1965; *Euglypha strigosa* (Ehrenberg, 1848) Leidy, 1878; *Trinema complanatum* Penard, 1890). The shells of species characteristic of early successional stages retain their presence subsequently, and the species richness is thus a function of time being constantly “accumulative”. In this case, aeroplankton serves as the most important source of protist cells (Finlay 2002; Wanner and Xylander 2005; Wilkinson et al. 2012).

Most of the rhizopod items found in the Tsey profile were represented by empty (dead) shells (Figs 6A, B). When analyzing the entire complex of identified species (live and dead cells), the alpha-diversity during the succession grows from 5 to 35 species, the Shannon index ranges from 1.2 to 3.0, the contribution of not too numerous (less than 12.5% of the total number) invaders to the overall taxocoenose loads usually makes up to more than 40% of the total abundance (Fig. 6E), and the composition of the community changes stochastically (Fig. 6C). When considering only live individuals, alpha-diversity along the transect increases from 2 to 18 species, the Shannon index varies from 0.4 to 2.6, and low-abundance species typically amount to less than 30% of the total abundance (Fig. 6F). During the succession of live rhizopods, a clear-cut increase in the species turnover was noted (Fig. 6D); the pioneer complex of

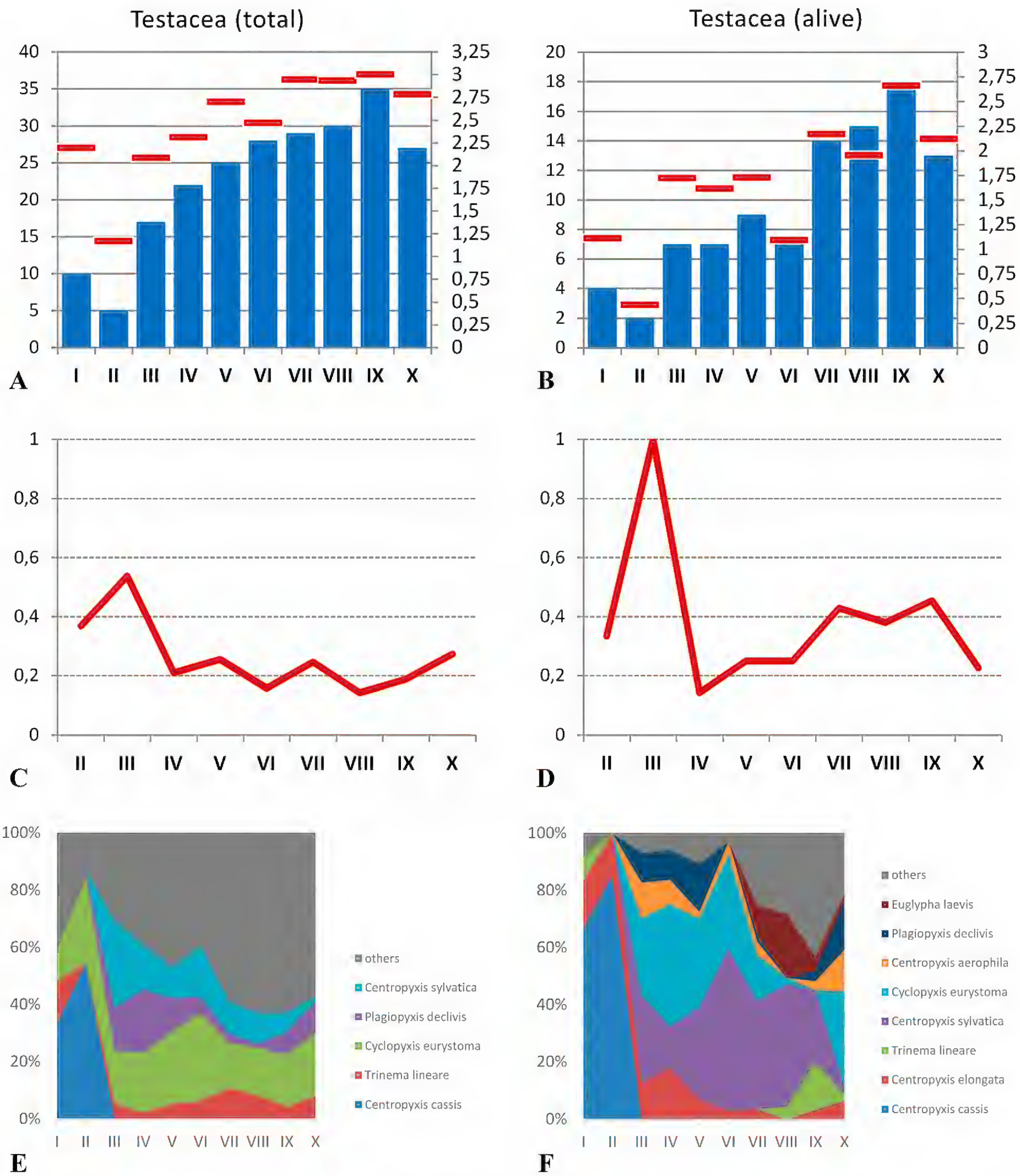


Figure 6. Comparison of species richness of testate amoebae communities and their dynamics along the profile, calculated for the full sample (left column) or only for live individuals (right column). **A**, **B**: number of species (blue bars, values plotted along the left ordinate) and the value of the Shannon index (red lines, values plotted along the right ordinate); **C**, **D**: Wilson-Schmida measure; **E**, **F**: change of dominant species.

species was replaced by the soil one; the latter was only slowly transformed later (Fig. 6F).

Earthworms (Lumbricidae). The earthworm fauna of the Caucasus includes at least 84 species, and the proportion of Caucasian endemics among them exceeds 60% (Kvavadze 1999; new unpublished data). At least 18 species occur

in North Ossetia – Alania, and in the Tsey Gorge proper, 5 species have been recorded, representatives of various genera (Rapoport and Komarov 2017). In general, in contrast to the enchytraeids found under the Tsey Glacier already on Plot II (i.e., 4 years following the surface exposure), the first Lumbricidae were noted at the shrub stage, Plot IV (14 years old), also found in all older communities of the study profile.

All specimens revealed belonged to one cosmopolitan boreal species: *Dendrobaena octaedra* (Savigny, 1826). In the North Caucasus, this is one of the most common earthworm species, living across a wide range of altitudes (Rapoport 2013). In the mountains, as well as on plains, *D. octaedra* prefers woodlands. Its colonization of new habitats is facilitated by the extreme cold-resistance of all development stages (Berman et al. 2002), parthenogenetic reproduction, small size, and litter lifestyle. It is this species that forms the main body of the invertebrate biomass in paraglacial biotopes in the Austrian Alps, but it was recorded there only 50–70 years following the glaciers' retreat (Janetschek 1949; Kaufmann et al. 2002). Near some Austrian glaciers, already 35 years after the exposure of the surface, a very small cosmopolitan *Bimastos rubidus tenuis* (Eisen, 1874), also reproducing parthenogenetically, was found. Later, both species often coexisted (Janetschek 1949).

In mature forest communities in North Ossetia, the earthworm diversity is generally low. Individual forests are usually inhabited by 1–5 species (Rapoport 2011); among them, in addition to the sylvan *D. octaedra* and *B. rubidus tenuis*, as a rule, there are also the Crimean-Caucasian endemics, *Dendrobaena schmidti* (Michaelsen, 1907) and *Dendrobaena nassonovi* Kulagin, 1889.

Mollusca. By the present time, more than 320 species of terrestrial molluscs have been recorded in the Caucasus, with two-thirds of them being endemics (Walther et al. 2014). There are several studies examining the altitudinal variability of the fauna (Shileiko 1969; Akramowski 1976; Kijashko 2000); however, there is a lack of specific research on the structure of high-mountain paraglacial gastropod communities.

It has been repeatedly observed that the diversity of terrestrial molluscs decreases with increasing elevation in the mountains, even in the absence of signs of current or past glaciation (Aubry et al. 2005; Cameron and Greenwood 1991; Horsák and Cernohorsky 2008; Sadouk et al. 2023), which is determined by winter temperatures and the duration of the frost-free period (Horsák and Chytrý 2014). However, the malacofauna of the Caucasus is characterized by a specific complex of endemic genera and species that inhabit exclusively the high-mountain belt up to an altitude of 3500 m a.s.l. (e.g., C*aucasolimax caucasicus* (Simroth, 1898) (Likharev and Wiktor 1980)).

The malacofauna of the Tsey profile is indeed not rich: only 18 species have been found at the dated sites, of which only four (22%) are endemic or subendemic to the region, while the remaining species are widely distributed in the Western Palaearctic territory, and the majority, 11 species (61%), are transpalaearctic.

As the glacier retreats, the first molluscs are observed only after 7 years (Plot III), against the background of the development of abundant grassland vegetation. This includes the specific alpine species *Caucasigena eichwaldi* (L. Pfeiffer, 1846), which occurs in the paraglacial belt up to an altitude of 3400 m a.s.l. (Walther et al. 2018) and represents an endemic genus and tribe Caucasi-

genini (Hygromiidae) for the Caucasus. This high-mountain species remains among the dominant species at plots III–V, disappearing in mature forests (Fig. 8B).

With the appearance of shrubs and the first litter layer (plot IV), several widely distributed species join it, such as *Vitrina pellucida* (O.F. Müller, 1774) or *Vertigo substriata* (Jeffreys, 1833). The diversity significantly increases in young forests (plot V), with a complex understory and developed leaf and moss litter. Here, the maximum species diversity (11 species) for the entire studied profile is recorded (Fig. 5A). The fauna includes both high-mountain Caucasian endemics characteristic of the alpine belt and a rich array of trans-Palaearctic eurybiontic species.

In forests older than 60 years, the complex of alpine endemics gradually drops out of the fauna, and the number of species decreases (usually to 6–8), with most of them being widely distributed eurybionts. At plot VIII, a dry pine-birch forest at the edge of the moraine, only three species of terrestrial gastropods were found. It has been noted multiple times that forests of this type are practically unsuitable for mollusc habitation (Kralka 1986; Wareborn 1992; Horsák and Hájek 2003).

Thus, the material of the Tsey chronosequence confirms the observation that the actual altitude above sea level does not affect the taxocoenoses of terrestrial gastropods (Mumladze et al. 2017). However, there is a clear consistency between phytocoenoses and snail communities, previously noted for other mountain systems (Horsák and Hájek 2003; Horsák et al. 2010). The screes and alpine grassland are populated by communities dominated by endemic high-mountain groups specific to the Caucasus; in the forest communities of the profile, formed by deciduous and coniferous trees, widely distributed species characteristic of the European southern taiga prevail. At the same time, the maximum diversity is observed in the transitional (between grassland and forest stages) biotope, the young forest (ecotone effect).

Acari. The first information concerning mites in the soil of paraglacial communities seems to have been obtained from the Austrian Alps (Kaufmann et al. 2002), but that was of little value in lacking a taxonomic treatment. All currently available data refer only to Northern Europe, including Svalbard (Hodkinson et al. 2004; Skubała and Gulvik 2005; Seniczak et al. 2006; Hågvar et al. 2009, 2020; Hågvar 2012; Gwiazdowicz et al. 2020), and to nunataks in Iceland (Ingimarsdóttir 2012). With the exception of the work of Gwiazdowicz et al. (2020) alone, all of them were devoted to oribatid mites, which are noted to be far from the first mite colonizers of the land freed from under the glacier (cf. Gryziak 2009). Apparently, it is geographical proximity that largely determines the similarity of the Northern European pioneer complexes of oribatids, these consisting of representatives of the genera *Liochthonius*, *Camisia*, and *Tectocepheus*, as a rule (Hodkinson et al. 2004; Skubała and Gulvik, 2005; Seniczak et al. 2006; Hågvar et al. 2009; Ingimarsdóttir 2012; Gwiazdowicz et al. 2020). The cold climate of this region seems to have caused the taxonomic poverty and slow development of oribatid communities, but even then, the diversity and abundance of the taxocoenose are steadily increased over time, and clear specific acarocoenoses are formed at different time stages (Skubała and Gulvik 2005; Seniczak et al. 2006; Hågvar et al. 2009; Gwiazdowicz et al. 2020).

We have processed the mite suborders Mesostigmata and Oribatida in particular detail. The dynamics of the remaining mite groups have been traced only in areas I–VI, where their species could only be identified to the genus level, as a rule, largely due to severe taxonomic problems.

Mesostigmata. Mesostigmatic mites in the Caucasus are still very poorly studied; the most complete information is related to plant-dwelling Phytoseiidae (Arutyunyan 1996; Murvanidze et al. 2019). The total diversity of Mesostigmata on the Tsey profile amounted to 61 species, of which 14 species (23%) are endemic to the Caucasus and 11 species (18%) represent species new to science (still to be described). The species richness and abundance of the taxocoenose constantly grow along the chronological row of biotopes (from 2 to 22 species) the proportion of endemics is especially high in the first stages (Fig. 5C), with which new representatives of the genera *Gaeolaelaps* Evans & Till, 1966; *Antennoseius* Berlese, 1916; and *Lasioseius* Berlese, 1916 are associated. At all stages of vegetation development, peculiar Mesostigmata communities are formed, although over time the turnover of species slows down (Figs 7C, D). The proportion of parthenogenetic species is consistently increased during succession (from 0 to 45%), and their contribution to the total abundance in the oldest areas reaches 61%. Taking into account the growing thickness of the litter layer (Table 3), which probably contains increasing amounts of prey and fungal mycelium, this can obviously be considered a further confirmation of the Structured Resource Theory, which describes the distribution of parthenogenesis (Maraun et al. 2019).

Oribatida. Oribatid mites have long been studied in the Caucasus, where more than a thousand species are presently known to occur (Shtanchaeva and Subías 2010). The fauna of Georgia alone comprises about 550 species (Murvanidze and Mumladze 2016; Murvanidze et al. 2019). However, of the 74 oribatid species found in the Tsey Gorge forests (including 68 species from the Tsey profile only), 10 (14%) belong to undescribed species. We can assume to have relatively completely discovered the oribatid fauna, since 86 species have been recorded along a forest transect in 9 habitats in Georgia (altitudes ranging 800–2200 m a.s.l.) (Mumladze et al. 2015). Endemics make up 20% of the species list in the Tsey Gorge, their share being especially large at the shrub stage in Plot IV (29% species). The first oribatids have been recorded only on Plot II (age 4 years) and, as in the most different pioneer communities of Europe, they are represented by the ubiquitous *Tectocepheus velatus* (Michael, 1880) and very small mites from the family Brachychthoniidae (Skubała and Gulvik 2005; Luxton 1982; Hågvar et al. 2020). The number of species is constantly increasing (from 0–5 at pioneer stages to 27–33 in mature forests), but even in the oldest areas (110–170-years old), it is almost half as much as in mid-montane Caucasian woodlands of Pleistocene age (Murvanidze and Mumladze 2014). The highest abundance of oribatids in our material was noted in the most mature forests of the study profile (290–580 ind./dm^2), which is some higher than the numbers in the mountain forests in neighboring Georgia, with not more than 250 ind./dm^2 (Mumladze et al. 2015).

Other mites. The poorly developed taxonomy of the huge order Trombidiformes (Prostigmata) and the suborder Endeostigmata, the lack of keys and specialists for most of the taxa they are composed of, coupled with the very small size of most species (200–400 μm), all this strongly hampers their

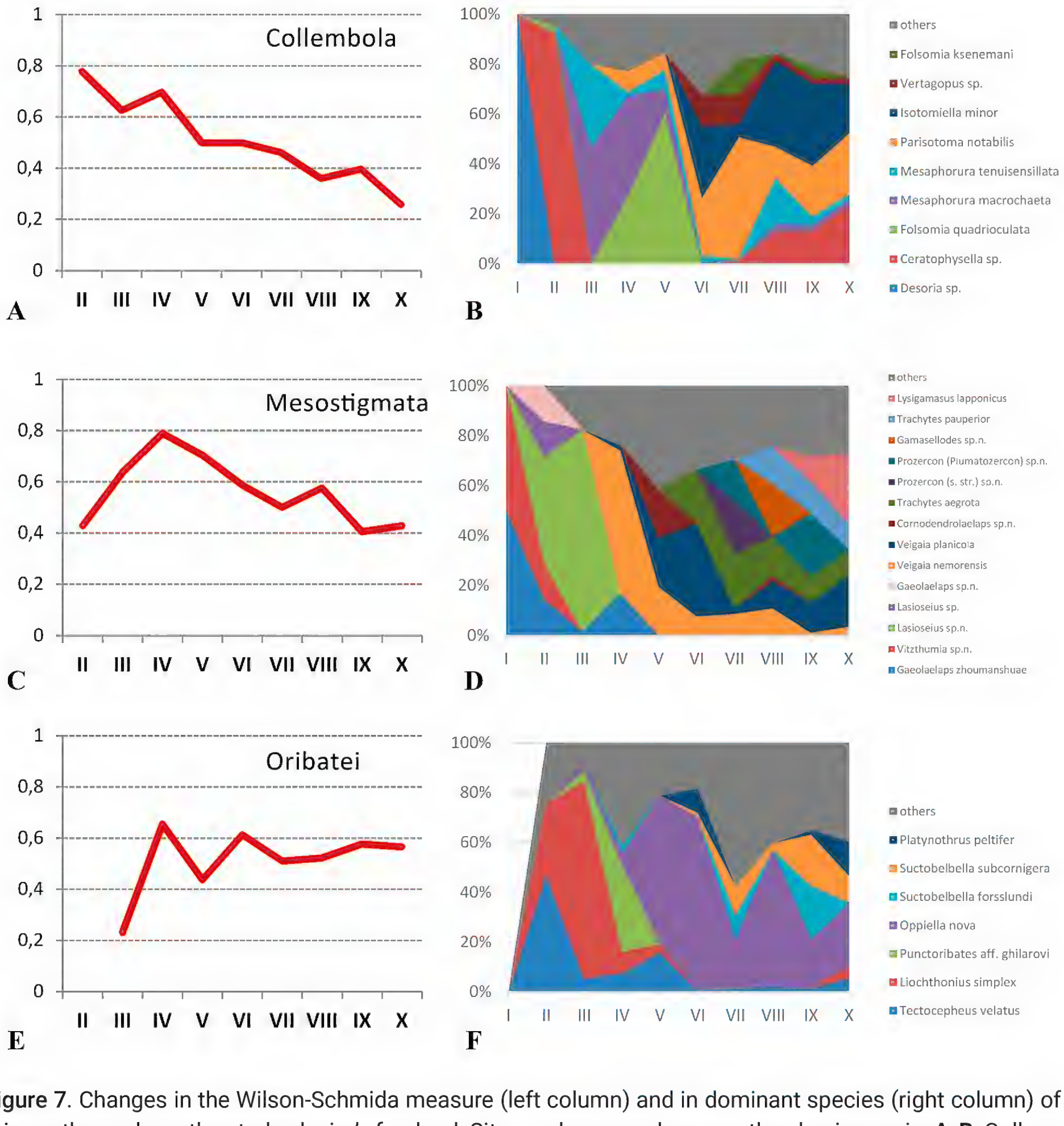


Figure 7. Changes in the Wilson-Schmida measure (left column) and in dominant species (right column) of microarthropods on the study glacier's foreland. Site numbers are shown on the abscissa axis. **A**, **B**: Collembola; **C**, **D**: Mesostigmata; **E**, **F**: Oribatei.

study globally. Yet, representatives of these very groups (mainly Eupodoidea, Tydeoidea, Nanorchestidae, and Alicorhagiidae) form the basis of the mite fauna and assemblages, starting with the first stages of the succession of paraglacial communities. The predominance of these very ancient (known from the Devonian) groups of mites is noted both in polar and arid deserts of both hemispheres (Makarova 2002, 2023). In the Tsey Gorge, in Plots I–VI, Prostigmata and Endeostigmata together account for almost 60% (88 species) of the mite list. On a one-year old site (Plot I), they strongly predominate (75% species, 88% individuals), and their share in the fauna and population in the next 60 years remains constantly high (28–65% species and 17–52% individuals). This has

also been noted under the retreating glaciers in the Subantarctic, where oribatid mites appear only 30 years later (Gryziak 2009). In our material from the Tsey Gorge, oribatids were recorded already 4 years following the glacier's retreat, but with the development of the community to a middle-aged forest (Plot VI), their share in the taxonomic diversity fluctuates only slightly (15–30%), and the contribution to the population of all mites is irregularly increased to 52%. Saprophilous astigmatic mites (suborder Astigmata), even species of the family Histiostomatidae that actively disperse on insects, appear on the profile only after 60 years with the formation of a profound humus horizon (Table 3).

Pseudoscorpiones. The highlands of the Caucasus (above 2000 m a.s.l.) are inhabited by at least 12 species of pseudoscorions, representatives of three families: Chthoniidae, Neobisiidae, and Chernetidae (Dashdamirov and Schawaller 1992). Everywhere, the largest number of species is represented by the subgenus *Neobisium* (*Neobisium*) (7 species in total), which is also typical of the highlands of Europe, where 16 species of this subgenus have been recorded (Beron 2002).

Along the glacier foreland of the Tsey Gorge, the first pseudoscorpions appear 60–70 years following the glacier's retreat (Plot VI), already in a mature birch forest with a developed litter and humus horizons (Fig. 2, Table 3). Everywhere, in Plots VI–X, a single species was recorded: the endemic North Ossetian *Neobisium* (*Neobisium*) cf. *vilcekii* Krumpál, 1983, which was described from the vicinity of Karmadon (Krumpál 1983; Kolesnikov et al. 2022) and later recorded also from the suburbs of Mozdok (Nassirkhani and Snegovaya 2021). Its abundance in the study Tsey profile is low, varying in the litter within the range of 0.1–0.7 ind./l; the lowest values were recorded in a stony pine forest on a moraine 96–100 years old (Plot VIII), the highest in a mature pine forest with a thick moss litter (Plot X, ≈170 years).

An opinion was expressed about the possible synonymy of *Neobisium* (*N.*) *vilcekii* and *N.* (*N.*) *labinskyi* Beier, 1937 (Dashdamirov and Schawaller 1992), but later it was not confirmed (Nassirkhani et al. 2020; Kolesnikov et al. 2022). Moreover, the variability of a number of morphological structures (Kolesnikov et al. 2022) indicates the need to use molecular genetic methods to study the status of this species. Thus, DNA barcoding used for *N.* (*N.*) *carcinoides* (Hermann, 1804), a species that lives throughout Germany (Muster et al. 2021), revealed high cryptic diversity at the species level, while many high-mountain populations turned out to be narrowly endemic. This, in turn, indirectly indicates the minimal dispersal capacities of representatives of the subgenus *Neobisium* (*Neobisium*), which may also determine their relatively late colonization of new paraglacial habitats.

Opiliones. Everywhere in Europe, during the retreat of glaciers, harvestsmen were observed already in the very first years, actively following the ice margin (Janetschek 1949; Hågvar and Flø 2015; Hågvar et al. 2020). Moreover, their numbers often exceed the abundance of the most typical pioneer groups of predators, such as ground beetles and spiders (Bråten et al. 2012; Hågvar and Flø 2015).

The fauna of the Caucasian Opiliones includes at least 85 species and is highly original (70% of the list are endemics). Along the study profile of the Tsey Gorge, in 10 principally different habitats, only six species have been recorded; this is significantly less than noted for the local faunas of the

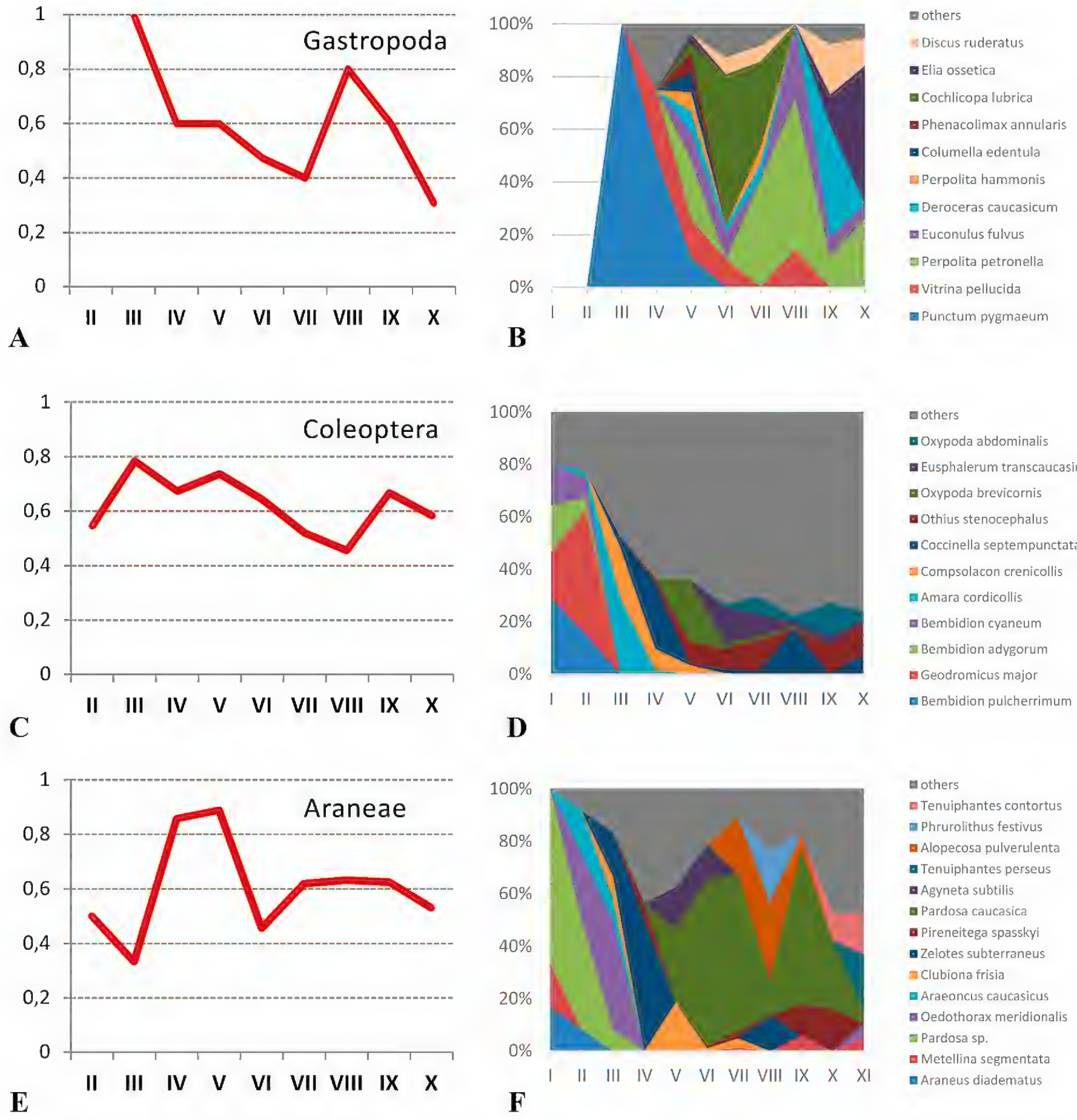


Figure 8. Changes in the Wilson-Schmida measure (left column) and in dominant species (right column) of mesopedobionts on the glacier's foreland. Site numbers are shown on the abscissa. **A**, **B**: Gastropoda; **C**, **D**: Coleoptera; **E**, **F**: Araneae.

low-montane areas in the Caucasus (13–16 species; Snegovaya and Chumachenko 2013, 2014).

Four of the six species were identified: *Paranemastoma kalischevskyi* (Roewer, 1951), *Odiellus zecariensis* Mkheidze, 1952, *Opilio lederi* Roewer, 1911, and *Metaplatybunus georgicus* Mkheidze, 1952. All of them are endemic to the Caucasus, with the same being likely for the two unidentified species.

An analysis of the composition of paraglacial taxocoenoses of Opiliones in the north and south of Europe indicates high regional specificity of the complex, even at the generic level (Janetschek 1949; Hågvar and Flø 2015; Hågvar et al. 2020), which is also confirmed by our data. For example, the absence of representatives of the genus *Mitopus* Thorell, 1976, whose species are com-

mon in paraglacial communities of both Northern and Southern Europe (Hågvar et al. 2020), is quite special to the study foreland profile.

As the Tsey Glacier retreats, harvestmen (adult wandering females) appear almost immediately. Each site in the profile is inhabited by only 1–3 species. That is, despite sharp changes in phytocoenoses with time (grassland, shrub forest communities), the Opiliones species diversity does not increase, something also observed in the Austrian Alps (Janetschek 1949). At the same time, the taxocoenose composition changes fundamentally. Thus, of the five species found at treeless stages (surface age up to 15 years old), three species fail to occur later. The forest species, *Paranemastoma kalischevskyi*, appears later than others (after 60 years). Then, for a century, only two characteristic Caucasian species (*P. kalischevskyi* and *Odiellus zecariensis*) lived in forests, regardless of forest type (pine forests, mixed and broad-leaved forests). The faunas of individual mature forests in the Caucasus, at altitudes up to 2000 m a.s.l., usually amounts to 7–16 species (Snegovaya and Chumachenko 2013, 2014). It cannot be excluded that the difference in species richness between postglacial and old-growth woodlands is due not only to the higher altitude of the Tsey Gorge but also to the limited opportunities for Opiliones settling. This is indirectly confirmed by the high level of their Caucasian endemism.

Along the Tsey Gorge postglacial profile, harvestmen become abundant only with the formation of a proper forest canopy. The largest number of specimens was obtained in Plot VI, a light ("park-like") 60-year-old birch forest, on a moraine between streams (in total, 172 ind., 1.2 ind. per pitfall per day). In the oldest of the study habitats with thick leaf litter or moss turf (Plots VIII–X), the abundance of Opiliones decreased.

Araneae. Spiders are one of the most conspicuous groups of arthropods in paraglacial communities (Janetschek 1949; Paulus and Paulus 1997). However, the first paper we know of, which is directly devoted to the study of the succession of arachnids under these conditions (Zingerle 1999), was carried out relatively recently in the Dolomites. Intense explorations performed in the Austrian Alps (Kaufmann 2001, 2002; Kaufmann et al. 2002; Kaufmann and Raffl 2002) demonstrated a very rapid change in arthropod groups, including spiders, at the initial stages of succession and a significant slowdown on older territories. The paraglacial complexes of Northern Europe most often include species of only two spider families, Lycosidae and Linyphiidae (Hodkinson et al. 2004; Vater 2006; Ingimarsdóttir et al. 2012); vs representatives of the family Gnaphosidae joining in at more mature sites (Franzén and Dieker 2014). Pioneer assemblages in the Alps are slightly richer, and, in addition to the three families mentioned above, they include some species of Theridiidae, Agelenidae, and Thomisidae (Kaufmann 2001; Gobbi et al. 2006a, b; Hågvar et al. 2020). At the same time, both in the northern and southern mountains, in the youngest areas, representatives of linyphiids and wolf spiders (Lycosidae) usually dominate in numbers.

In total, at the dated sites of the Tsey Gorge, we identified 39 species of spiders, of which two species (or ~5% of the total list) have not yet been described. Pioneer assemblages of spiders of comparable age along the Tsey profile are noticeably more diverse than those in the highlands of the Alps, not only in the number of species but also in the family array. We noted representatives of seven families, i.e., Araneidae, Clubionidae, Tetragnathidae, Saltici-

dae, Gnaphosidae, Linyphiidae, and Lycosidae, already at the grassland stage (surface age not more than 7 years). There were only a very few species common to the paraglacial communities of the Caucasus, the European Alps, and northern Europe. Thus, only two of the species we discovered, *Agyneta rurestris* (CL Koch, 1836) and *Erigone dentipalpis* (Wider, 1834), were recorded in similar conditions of the Italian Alps (Gobbi et al. 2006a, 2017; Tampucci et al. 2015; Bernasconi et al. 2019), and only one, *Zelotes subterraneus* (CL Koch, 1833), in northern Europe (Vater 2006). At the first stages of succession, not only such a peculiar high-montane species as *Pardosa* aff. *ibex* was recorded, but also several forms with a wide altitudinal range, confirming the high potential of the group in the paraglacial conditions studied. At the same time, the pioneer complex of spiders turned out to be rather short-lived: at a 14-year-old site (a shrub stage), it was almost completely replaced. In the young mixed forest (following another decade), it reached a diversity level that is quite comparable to those in developed communities of the mountain forest belt in the Caucasus (Babenko and Ponomarev 2023). Endemic species (3 species, 7.7% of the list) were recorded both in the grassland (1) and forest (2) parts of the profile.

Chilopoda. Paraglacial taxocoenoses of Chilopoda have previously been studied only in the Italian and Austrian Alps (Janetschek 1949; Kaufmann 2001; Kaufmann et al. 2002; Gobbi et al. 2006b, 2020). Different works indicate two to 11 species, all of which belong to the order Lithobiomorpha and the family Lithobiidae. The share of endemic species is up to 18%, but polyzonal eurybionts dominate numerically (Gobbi et al. 2020). In the Alps, the widespread European *Lithobius lucifugus* L. Koch, 1862, is a common pioneer species. It can even occur on the glacier surface covered with rock debris (Gobbi et al. 2011, 2020), although the first lithobiids are usually to appear on moraines older than 60 years (Gobbi et al. 2006b). A change in their trophic spectrum during postglacial succession has been shown based on the results of isotope analyses (König et al. 2011). In general, in the Alps, most Chilopoda species avoid high-altitude areas, preferring mature forest soils in the mid-mountains, where up to 26 species can live together (Peretti and Bonato 2018; Gobbi et al. 2020). In the Caucasus, up to 10 lithobiid species have been found in individual mountain forests (Zalesskaya 1978).

In the chronological series of communities formed during the Tsey Glacier's retreat (Table 1), six species of Chilopoda were revealed, all of them belonging to the genus *Lithobius* Leach, 1814. At the grassland and shrub stages of succession, only one species was noted: *Lithobius sseliwanoffi* Garbowski, 1897, which was first found on a 7-years-old plot (III) wealthy in small reeds and legumes. In the Caucasus, this common, widespread eurybiont species has been recorded to inhabit different successive forest communities for at least a century, but has not been found in the oldest (≈ 170 years old) pine forest (Plot X) with a thick moss turf. In most forest habitats, one or two species were revealed, and the greatest species diversity (four species) was observed in the middle part of the profile, in a rocky 100-years-old pine forest on a moraine ridge (Plot VIII) with an undergrowth of small-leaved tree or bush species and rhododendron. Most of the species found on the profile are polyzonal eurybionts. The only exceptions are endemic to the Caucasus: *L. striatus monosulcatus* Folkmanova, 1958, characteristic of forest habitats (Zalesskaya 1978), and *L. evsyukovi* Zuev, 2017, so far known only from the mid-mountain belt of

North Ossetia – Alania (Zuev 2017). Both of these species on the Tsey profile are confined to middle-aged woodlands, birch and pine forests, respectively.

Diplopoda. The species endemism of the millipede fauna both of the Caucasus in general (including >80% endemics and subendemics) and North Ossetia – Alania in particular (nearly 90%) is profound (e.g., Kokhia and Golovatch 2020). The development of their paraglacial communities has been traced in the Austrian and Italian Alps (Janetschek 1949; Kaufmann 2001; Kaufmann et al. 2002; Gobbi et al. 2011; König et al. 2011), but never in Russia.

In the Alps, a good number of diplopod species appear to demonstrate an upslope shift by 50–350 m over the last 100 years against the background of a 1.5 °C increase in the mean annual temperature (Gilgado et al. 2021). Warming can thus lead to habitat fragmentation and even the extinction of such low-vagile arthropods as millipedes.

Along the entire Tsey Gorge profile of postglacial habitats, only three diplopod species have been recorded. Two of them, *Byzantorhopalum rossicum* (Timotheew, 1897) and *Omobrachyiulus caucasicus* (Karsch, 1881), dwelling in different altitudinal belts of the Caucasus, were found already at the shrub stage (Plot IV, surface age 14 years old). It was at this stage that the first leaf litter and moss turf were formed, but the pine trees had not yet appeared.

Later, in mixed and coniferous forests, millipedes are virtually absent. A few specimens of *B. rossicum* and *Julus jedryczkowskii* Golovatch, 1981, were found only in a mixed, century-old forest (Plot IX), while in the close-located maple forest (outside the profile), diplopods were more diverse and abundant. In paraglacial communities of the Austrian Alps, the composition of communities is principally different, even at the generic level. After glacier retreat, diplopods appear within 17–40 years, but stable complexes of these important forest-floor decomposers are formed only after 70–90 years (Janetschek 1949; Kaufmann 2001; Kaufmann et al. 2002; König et al. 2011). The probable causes for such a late colonization of postglacial forests by millipedes seem to be rooted in their relatively low mobility. Apparently, this feature is also responsible for the high-level endemism characteristic of this group, which determines, at the generic level, the high regional specificity of their paraglacial taxocoenoses. Yet, the low diversity of diplopods in the study profile can be a good measure, apparently because of the high elevations and unsuitable litter quality. Local millipede fauna in low-montane areas in the West Caucasus can comprise 16–32 species, and only one forest plot, the relict boxwood or some broadleaved forest, can be populated by 16–27 diplopod species (Chumachenko 2016; Korobushkin et al. 2016).

Collembola. Early investigations of paraglacial springtail communities were carried out in the Austrian Alps (Janetschek 1949; Kaufmann et al. 2002), as well as in Scandinavia (Hodkinson et al. 2004; Hågvar 2010, 2012) and on nunataks in Iceland (Ingimarsdóttir 2012). Recently, the first studies were conducted in the highlands of Italy (Valle et al. 2022), and global reviews of the data on primary paraglacial communities were published (Hågvar et al. 2020; Hågvar and Gobbi 2022). In all study areas, springtails are among the first colonizers of deglaciated surfaces. This group is also often mentioned as prey for pioneer macrofauna (König et al. 2011; Raso et al. 2014; Sint et al. 2019; Hågvar and Gobbi 2022), indicating its key role in the establishment of primary ecosystems.

The species composition of paraglacial springtail assemblages varies considerably, even within the same region (Hågvar et al. 2020). As a rule, they are composed mainly of local hygrophilic forms with an admixture of atmobiontic species. Among the pioneer species, cryophilic Isotomidae are found everywhere, being clearly adopted to life near or directly on the glacier surface (Gwiazdowicz et al. 2020; Hågvar et al. 2020; Valle et al. 2022).

Altogether, 73 collembolan species were revealed on the study profile under the Tsey Glacier, of which at least 7 species (9.6%) have not been described yet. A postglacial succession of springtail communities in the Tsey Gorge (and possibly in the Central Caucasus as a whole) starts with a clearly cryophilic undescribed species, *Desoria* sp. aff. *duodecimoculata* Denis, 1927. Already on a one-year-old surface, both adults and juveniles of this species are found, clearly indicating its reproduction in that habitat. Outside Plots I and II, i.e., after the appearance of a pronounced vegetation cover, this species has not been recorded (Antipova and Babenko 2023a).

During the first years of succession, rapid changes in the species composition and community structure occurred. At the shrub stage (14 years), a sharp increase both in total abundance and species diversity was observed. Starting from this stage, the main part of the springtail assemblages consists of omnipresent eurybiontic species, often with wide geographical distributions, while the species diversity ranges from 25 to 35 species. The rate of succession gradually slows down in the forest stages. After about 100 years, the springtail assemblages reached a level of diversity similar to that found in mature mountain forests in the region (Kuznetsova et al. 2019).

Among the springtails of the Tsey Gorge, only eight species can be securely classified as Caucasian endemics, amounting to only 11% of the total list. All of them are only confined to a certain successional stage (grassland, shrub, or forest stages). A special position on the profile is occupied by the pioneer species *Desoria* sp. aff. *duodecimoculata*, which inhabits exclusively bare ground at the very edge of the ice. In addition to North Ossetia, this species (or possibly a form very close to it) has already been recorded from the foreland and directly on the ice surface of several glaciers in Kabardino-Balkaria (Bezenghi, Mizhirghi, Kashkatash, and Bashkara).

Coleoptera. Beetles, primarily ground beetles, are one of the most popular groups in studies on paraglacial communities. It was their (together with spiders) high visibility on young surfaces that determined the development of the concept of “the predator’s first paradox” (Kaufmann 2001; Hodkinson et al. 2002; Hågvar and Gobbi 2022).

Analyses of beetle successions after glacial retreat in different regions of the world show very different patterns (Janetschek 1949; Kaufmann 2001; Gobbi et al. 2006b; Bråten et al. 2012; Vater 2012; Moret 2020; Rosero et al. 2021; etc.). It is largely dependent on the natural zone involved (and, consequently, the altitude of the glacier edge), the presence of grazing, the abundance of ants, and, especially, the involvement in the analyses of representatives of Staphylinidae; Their study faces particularly numerous problems.

In ten study plots of the Tsey postglacial profile, using various trapping techniques, 121 species of beetles have been revealed, which is only a third less than the diversity collected over a similar altitudinal range during three-

year-long surveys in the Austrian Alps (Lang 1975), yet significantly more than the number recorded along a postglacial profile in southern Norway, where in 3–205-year-old habitats at altitudes of 1300–1400 m a.s.l. during two summer seasons, only 40 species of ground-dwelling beetles were found (Bråten et al. 2012). Moreover, the number of beetle species discovered along the postglacial profile of the Tsey Gorge (121 species) is at least half as high as the list of the coleopteran fauna of the entire Tsey Gorge (more than 243 species; Alekseev 1986). It is difficult to compare the diversity of beetles in our material with similar studies in the southern European mountains since they all failed to include data on the most diverse family, Staphylinidae (Kaufmann 2001, 2002; Gobbi et al. 2006b, 2011).

All beetles in the Tsey profile have been precisely identified to the species level and appear to belong to 13 families, among which the most diverse are Staphylinidae, Carabidae, and Curculionidae (64, 30, and 11 species, respectively). Among the species found, almost half (42.8%) are Caucasian endemics (Kryzhanovskij et al. 1995; Penev and Alekseev 1996; Davidian and Savitsky 2006; etc.). These are present in all habitats, but at the pioneer stages, they form the main body of the group. It is noteworthy that, among ground beetles, Caucasian endemics are represented both by grassland and forest specialists, distributed respectively along the profile. Among Staphylinidae, most of the endemics (13 species, 81.2%) are associated with forest plots in the profile (up to 8 species in Plots VI and X). Most of the beetle species found (68%) are capable of flight, while the pioneer groups almost entirely consist of good flyers; this has already been noted for young high-altitude coleopteran faunas in the Scandinavian mountains (Nilsson et al. 1993; Bråten et al. 2012), but far from always corresponds to the situation in paraglacial carabid communities in the Alps (Gereben 1995; Chamberlain et al. 2020). The stable conditions of mature humid forests sometimes selectively support wingless ground beetle species (Gobbi et al. 2006b).

In individual habitats, from 8 to 43 species of ground-dwelling beetles were found, and the highest values were noted in 60–75-year-old forests. In the oldest woodlands of the profile (Plots IX–X), only 23–25 species occurred, which is half as many as found in the forests located somewhat below the terminal moraine of the mid-19th century in the Tsey Gorge (Alekseev 1986). Yet, a decrease in beetle diversity in the later stages of postglacial succession has been noted in a variety of regions (Bråten et al. 2012; Pothula and Adams 2022).

Predatory beetles (Carabidae, Staphylinidae) appear immediately after the surface becomes exposed. The core of this primary complex consists of the rove beetle, *Geodromicus major* Motschulsky, 1860, endemic to the Caucasus, and the ground beetles that represent the genera *Bembidion* Latreille, 182, *Nebria* Latreille, 1825, and *Cicindela* Linnaeus, 1758. All these species are predators and necrophages, characteristic of the high-montane riverine pebbles of the Caucasus and Europe. Many species from these genera are common in the pioneer stages of postglacial succession (Gereben 1995; Kaufmann 2001; Schlegel and Riesen 2011; Bråten et al. 2012; Hågvar 2012; Matthews and Vater 2015; Gobbi and Lencioni 2020). Of particular interest is the record in Plot I (and only there) of the rare *Deltomerus komarovi* Zamotajlov, 1988, which can probably be considered a local endemic of the Tsey Gorge and the surrounding mountains (Zamotajlov 1988; Kryzhanowskij et al. 1995).

At the early stages of succession (Plots II and III with herbaceous vegetation), there is a massive development of the widespread burrowing rove beetle, *Bledius opacus* (Block, 1799), and, among ground beetles, of the granivorous subendemic *Amara cordicollis* Ménétriés, 1832, and predators from the genera *Poecilus* Bonelli, 1810, and *Notiophilus* Duméril, 1806. All of them fully disappear after a decade. In addition, mass encounters of click beetles, Elateridae, are confined to grassland associations. These are the Eastern Mediterranean *Compsolacon crenicollis* (Ménétriés, 1832) and the South European-Caucasian *Zorochros quadriguttatus* (Laporte de Castelnau, 1840); both are zoo- and necrophagous species (Penev and Alekseev 1996).

Only 60–80 years later, in mature forest communities, wingless species of rove beetles were observed. It is also then that the forest species of ground beetles that are endemic to the Caucasus, *Carabus fossiger ingusch* (Zolotarev, 1913), *Leistus fulvus* Chaudoir, 1846, and *Pterostichus caucasicus* Ménétriés, 1832, start regularly to be found. Important components of the diet of these carabid beetles are molluscs and/or earthworms on the forest floor. Forest-dwelling members of the genera *Cychrus* Fabricius, 1794, *Carabus* Linnaeus, 1758 and *Pterostichus* Bonelli, 1810, belong to the endemic or subendemic (Caucasus + Turkey) subgenera *Pachycarabus* Gehin, 1876; *Tribax* Fischer von Waldheim, 1817; *Cechenochilus* Motschulsky, 1850; *Eurymelanius* Reitter, 1896; and *Myosodus* Fischer von Waldheim, 1823. Representatives of the genera *Carabus* and *Pterostichus* are well known as late colonists of postglacial surfaces (Gobbi et al. 2006b, 2011, 2017; Gereben-Krenn et al. 2011; Bråten et al. 2012; Vater and Matthews 2015; Hågvar et al. 2017; Lencioni and Gobbi 2018).

Phytophagous Curculionidae are absent from the pioneer stages, and the first representatives of this family appear in the grassland area (Plot III). Among them, members of the genus *Otiorhynchus* Germar, 1822 predominate (8 of 11 species, 73%). All of them are wingless, and almost all are endemic to the Caucasus. It seems noteworthy that most *Otiorhynchus* species found belong to subgenera that are widely represented in the mountains of Central Asia, the Caucasus, Anatolia, and, partly, Southern Europe (*Eprahenus* Reitter, 1912; *Namertanus* Reitter, 1912; *Otismotilus* Reitter, 1912; *Proremus* Reitter, 1912). Specialized species of the subgenus *Namertanus*, which is characterized by a transition to an endogeic lifestyle (Davidian and Savitsky 2006), appear only in the forest plots.

Taking into account only a small number of species of the other families of Coleoptera, we can conclude that: (**1**) at the pioneer stages (Plots I–II), a highly specialized oligodominant community is formed, consisting of well-flying predatory species, most of which (75%) are endemic to the Caucasus; (**2**) starting with the grassland stage (Plot III), phytophages appear and the proportion of wingless species is increased, reaching the maximum values in forests; (**3**) the formation of forest beetle communities is accompanied by the disappearance of most species of open habitats, this leading to a decrease in species richness and endemism (25%) of the beetle composition in young forests (Plot V); (**4**) as forest communities with a polydominant structure are developed, the overall diversity and proportion of endemic species again grow (up to 70% in mature forests), but wingless endemics predominate (up to 80–100%) at this stage.

Small mammals. The only small mammals captured by soil traps were shrews. They were found beginning in Plot IV (age 14 years) with complex

shrub vegetation, rich forbs, and moss sods, where for the first time a pronounced litter horizon was noticed on the profile (Tables 2, 3). Starting from the same stage, arthropod parasites of shrews were recorded in the traps (fleas, ticks, and gamasid mites). In all habitats, *Sorex volnuchini* Ognev, 1921, predominated (15 of 17 individuals), and two animals are identified as *Sorex satunini* Ognev, 1922. Volnukhin's shrew is the smallest species among the three species of the genus *Sorex* living in the Caucasus. In the monograph by Sokolov and Tembotov (1989), Volnukhin's shrew is characterized as an eurytopic species inhabiting the foothills, forest belts, and alpine grasslands up to 3000 m a.s.l. This species is marked for sharp irregular outbreaks in abundance, which can occur in different altitudinal belts, while its abundance can be several times higher than the total abundance of other shrew species (Sokolov and Tembotov 1989). The reasons for the sharp increase in the number of Volnukhin's shrews have not been studied. However, they were investigated for an ecologically and genetically similar species, the Eurasian pygmy shrew (*Sorex minutus* L., 1766). An increase in its numbers was observed with a decrease in the overall abundance of the shrew community (Ivanter 1976; Sheftel 1989), when competitive relationships between species weakened. It can be assumed that, as the glacier retreats, new territories are quickly populated by less competitive pioneer species. Besides this, the small species of shrews collect invertebrates from the soil surface, while earthworms remain out of their food spectrum (Churchfield and Sheftel 1994). Other main groups of soil invertebrates (collembolans, spiders, harvestmen, insects, and their larvae) appear almost immediately during glaciers' retreat (Table 4). The slow increase in earthworm populations appears to limit the penetration of other shrew species into these habitats.

Conclusive remarks

The number of studies on paraglacial successions steadily grew over the past 30 years, although animal assemblages, mainly invertebrate ones, were studied less intensely than vegetation and microbial communities (Ficetola et al. 2021). Such a situation was to some extent considered to reflect the identification problems due to the lack of taxonomists. Our material from the Tsey Glacier foreland has been subjected to a comprehensive taxonomic treatment. Identifications of a wide range of larger taxonomic groups (including the enormously species-rich beetle family Staphylinidae), coupled with the use of a range of invertebrate collection methods, have allowed us to assess the species richness of the fauna most completely. In total, 437 species of invertebrate animals were identified, which is 78–98% of the expected number of species for different groups (Table 4). The greatest diversity, as one would expect, has been revealed in the insect order Coleoptera, or beetles (Fig. 4).

When analyzing foreland successions, the pioneer species complex has only rarely been treated from such an early stage and so fractionally as in our material. Moreover, data comparisons are often complicated by different understandings of the duration of a pioneer phase of succession (Hågvar et al. 2020). Yet the available information and our results allow for a significant universality of the pioneer array of genera to be discussed for ground beetles, centipedes, pseudoscorpins, and mites, and a much greater regional specificity for molluscs, spiders, harvestmen, and springtails. In our material, almost all dom-

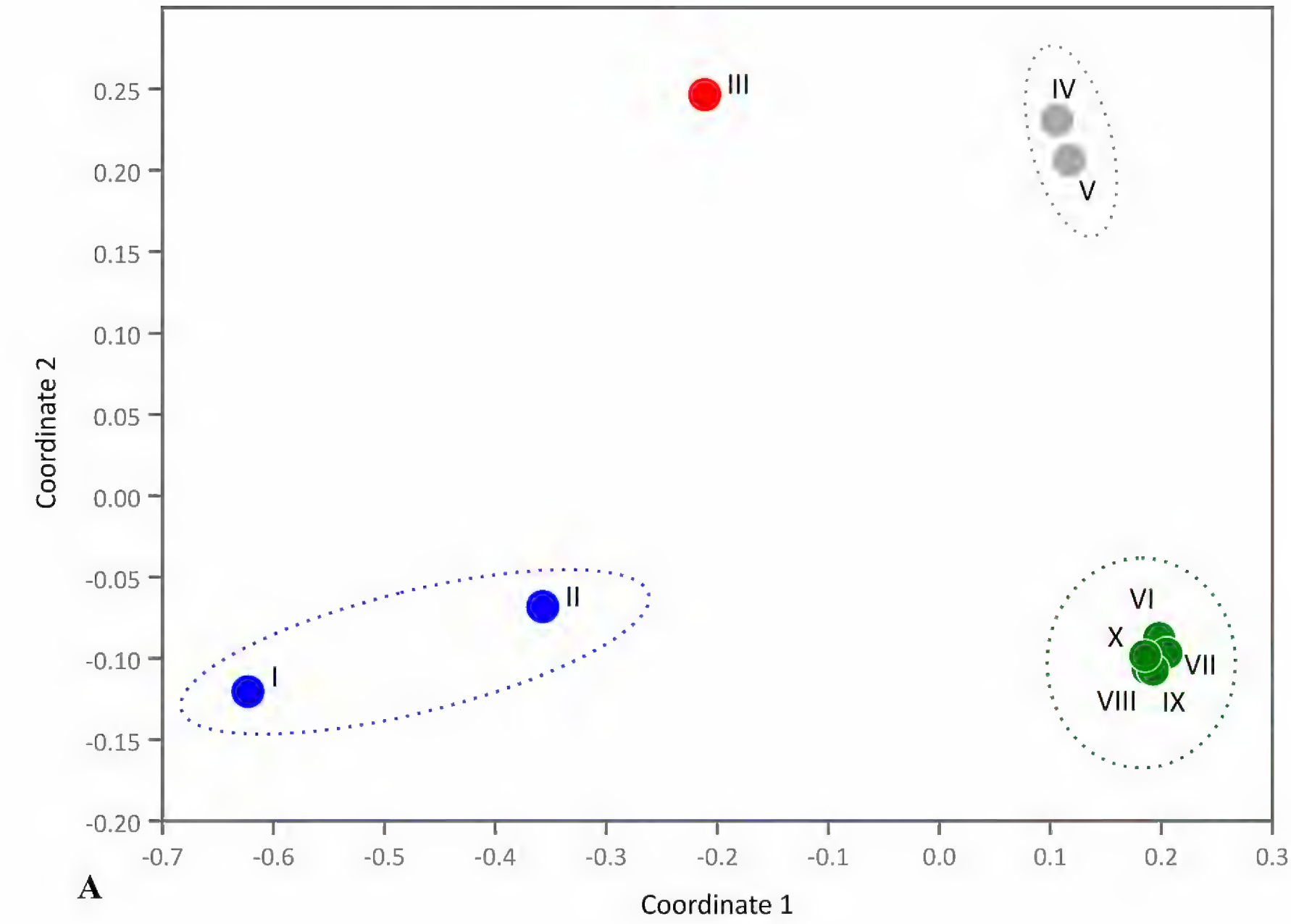
inant species of the pioneer stages (Plots I–III) are high-montane specialists endemic to the Caucasus. These are mainly members of the genera *Lasioseius*, *Antennoseius* (Acari), *Pardosa* (Araneae), *Ceratophysella*, *Desoria* (Collembola), *Bembidion*, *Amara*, and *Geodromicus* (Coleoptera).

Testate amoebae, various groups of mites, springtails, spiders, harvestmen, Carabidae, Staphylinidae, and shore bugs (Saldidae) appear on ice-free surfaces almost immediately, during several months (Table 5). Microarthropods that are incapable of flight can be effectively dispersed by air currents (Ingimarsdóttir 2012; Flø and Hågvar 2013). In the absence of plants, this complex can be stably maintained by both the autochthonous microbiota and the allochthonous input of detritus and newly arriving organisms (Ficetola et al. 2021; Hågvar and Gobbi 2022). Thus, replacing the classical "predator first paradox" principle (mainly following the footsteps of Hodkinson et al. 2001, 2002) with the recently proposed "Collembola first principle" (Hågvar et al. 2020; Hågvar and Gobbi 2022) seems inappropriate for our study in the Central Caucasus, since on new terrain the multi-taxa and multi-guilds invertebrate community emerges as a whole almost immediately.

There seems to be little sense in trying to assess the order of importance of such factors as the dispersion capabilities (colonization), environmental filter (vegetation and soil quality), and intraguild competition without field experiments (Vater and Matthews 2015; Rosero et al. 2021). These factors appear to be too strongly interconnected and act simultaneously. It is obvious that the habitation of such saprophilous forms as actively phoretic mites of the astigmatan family Histiostomatidae and well-flying representatives of Blattoptera (forest cockroaches) in mature forests is primarily determined by environmental conditions (probably microclimate and/or humus quality). Besides this, colonization in general is not a limiting factor for very small organisms (Finlay 2002). Thus, it is interesting to note that among the ubiquitous testate amoeba, *Centropyxis cassis* (Wallich, 1864) appeared in our material to be an absolutely pioneer species, whose shells, both live and dead, have been found only on Plots I–II (1–4-year-old sites). However, on Svalbard glacier's foreland, in the cold conditions and species-poor surroundings, this species remains eudominant in position over at least 150 years (Hodkinson et al. 2004), possibly being a non-pioneer cryophile.

Invertebrate assemblages of different succession stages show a clear division into four large clusters, even using different clustering methods, that are in full accordance with the trajectory of community development without any signs of stochasticity (Fig. 9). Thus, the community assembly in our case is, without doubt, a deterministic (predictable) and directional process in the sense of Kaufmann (2002) and Hodkinson et al. (2004). Changes in dominant species in our material occur gradually (Figs 6–8), contradicting some patterns observed in the Alps (Janetschek 1949; Kaufmann 2001; Gobbi et al. 2006b), where a rapid development of pioneer communities is followed by a greater turnover at older stages almost without species overlap.

There are some ideas about two fundamentally different types of change in foreland communities (Vater and Matthews 2015). According to 'the addition and persistence' model of invertebrate succession, deglaciated terrains



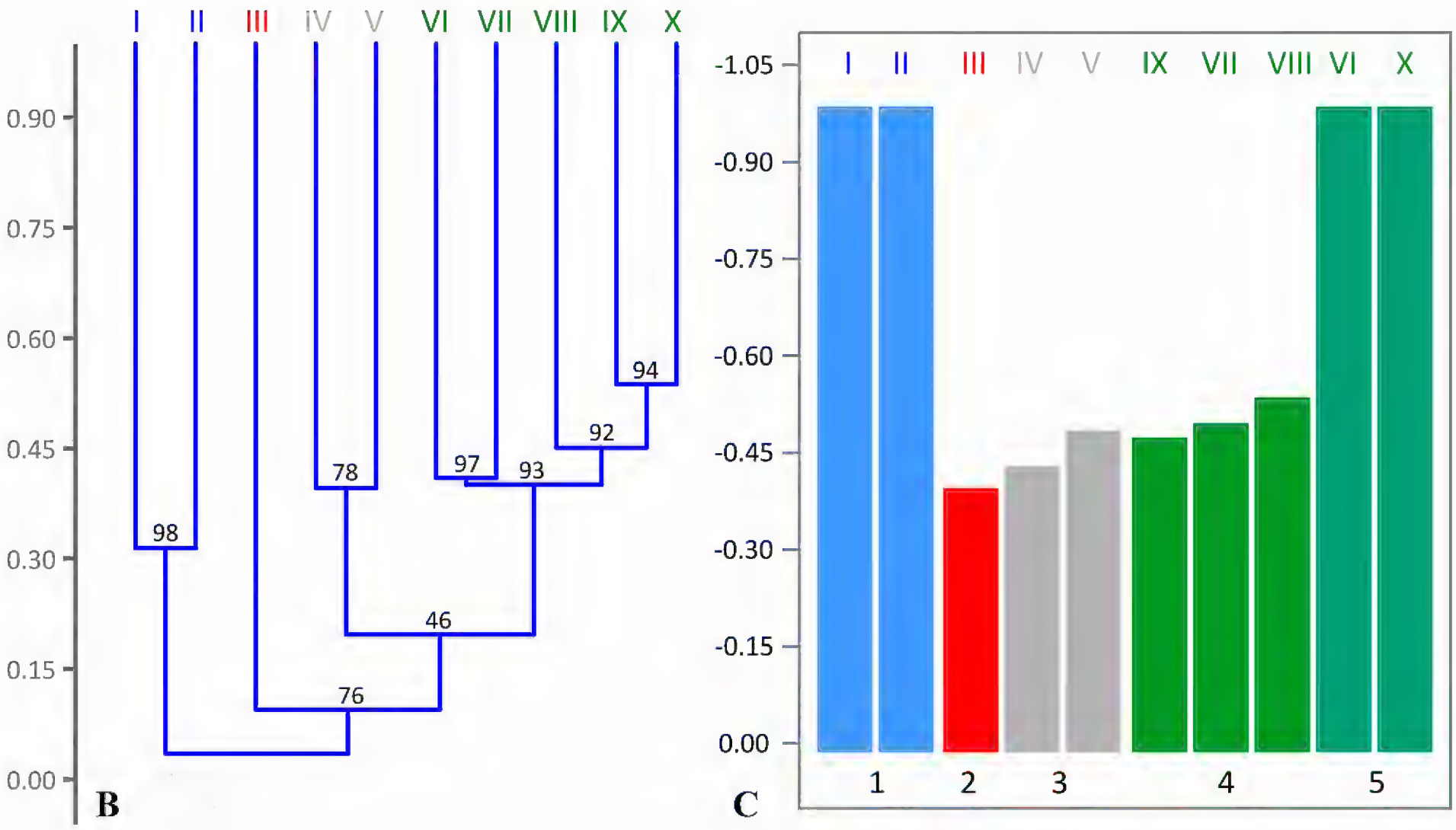


Figure 9. Classification of the study communities based on the Bray-Curtis similarity coefficient. **A**: non-metric ordination (stress factor 0.08852); **B**: hierarchical cluster analysis (UPGMA clustering method, nodes showing bootstrap values); **C**: flat cluster analysis (k-medoid clustering).

are colonized by pioneer species that persist from the early stage to the oldest one, gradually accompanied by an increasing number of new colonists (Vater 2012). On the contrary, following the 'replacement model', these are discrete invertebrate communities that are replaced along the chronosequence (Janetschek, 1949; Kaufmann 2001; Gobbi et al. 2007; Schlegel and Riesen 2011; etc.). Yet, additions can prevail at the earliest stages, but later the number of replacements can grow due to resource limitations and increased competition (Ficetola et al. 2021).

On the study postglacial profile in the Tsey Gorge, the development of all investigated taxocoenoses proceeds with a high species turnover in accordance with the 'replacement model' of succession (Table 6; Figs 6–8). Some features of a nestedness component in structural changes are demonstrated by only three groups of organisms studied, namely, the passively dispersed testate amoebae and the poorly diverse harvestmen (Opiliones) and centipedes (Chilopoda). A prevalent nestedness component, manifested in the accumulation of species during succession (due to the 'addition and persistence model'), is characteristic of passively dispersing taxa (Rosero et al. 2021) being often observed in cold conditions, when the surrounding natural communities are poor in species and therefore the competition between species is weakened (Vater 2012; Tampucci et al. 2015; Vater and Matthews 2015; Moret et al. 2020).

The recently suggested idea that foreland communities change only through replacement or addition following glacier retreat is an oversimplification (Ficetola et al. 2021). The inconsistent information accumulated to date, including thoughts about the changing patterns during succession, makes it almost impossible to search for some general patterns that are appropriate for different taxa and regions (Ficetola et al. 2021; Pothula and Adams 2022).

In the European Alps, the study of post-glacial succession is further complicated by the influence of pasturing and ants (Vater 2012). Moreover, the traditional use of only one collection method can significantly distort our ideas about the structure and dynamics of foreland communities (see, for example, comments in Antipova and Babenko (2023b) and Valle et al. (2023)). Thus, apparently, the theoretical constructions attributable to foreland invertebrate successions are still premature. They should be based on high-quality background information based on detailed species identification obtained using complementary collection methods, as well as on data on multiple taxonomic groups simultaneously.

Usually the strongest changes in the structure of foreland communities have been observed in the first 20–50 years (Ficetola et al. 2021; Pothula and Adams 1922; Cantera et al. 2023), this being clearly visible in our material as well (Figs 6–8). A reduction in the substitution rate, as revealed by the Wilson and Shmida index, is noted almost in all groups (Figs 6–8). When analyzing the general pool of data, with a continuing trend of growth in overall species diversity, at the last stages, the number of species disappearing from the community has also been found to start exceeding the number of those appearing for the first time (Fig. 10). Inhibition of postglacial succession has been observed both in botanical and zoological studies (Ficetola 2021; Cantera et al. 2023). It is intense grazing and the plenty of ants that have been suggested to cause the damping of succession in the highlands of the Alps (Vater 2012). In the territory of the Tsey Nature Reserve, the post-glacial communities are restored without human dis-

Table 6. Multiple-site Sørensen β-diversity, with both turnover and nestedness components calculated for all communities (Tsey Glacier foreland, Central Caucasus, July 2021). Turnover component measured as Simpson dissimilarity; value of the nestedness component measured as nestedness-resultant fraction of Sorensen dissimilarity; value of the overall beta diversity measured as Sorensen dissimilarity.

	All	Testacea (alive)	Gastropoda	Oribatida	Mesostigmata	Opiliones	Aranei	Chilopoda	Collembola	Coleoptera
Turnover component	0.9864	0.7433	0.7785	0.9132	0.9190	0.6364	0.9091	0.6429	0.8974	0.9653
Nestedness component	0.0068	0.1494	0.0936	0.0466	0.0410	0.1818	0.0361	0.1720	0.0568	0.0145
Sørensen dissimilarity	0.9933	0.8926	0.8721	0.9598	0.9601	0.8182	0.9452	0.8148	0.9541	0.9799

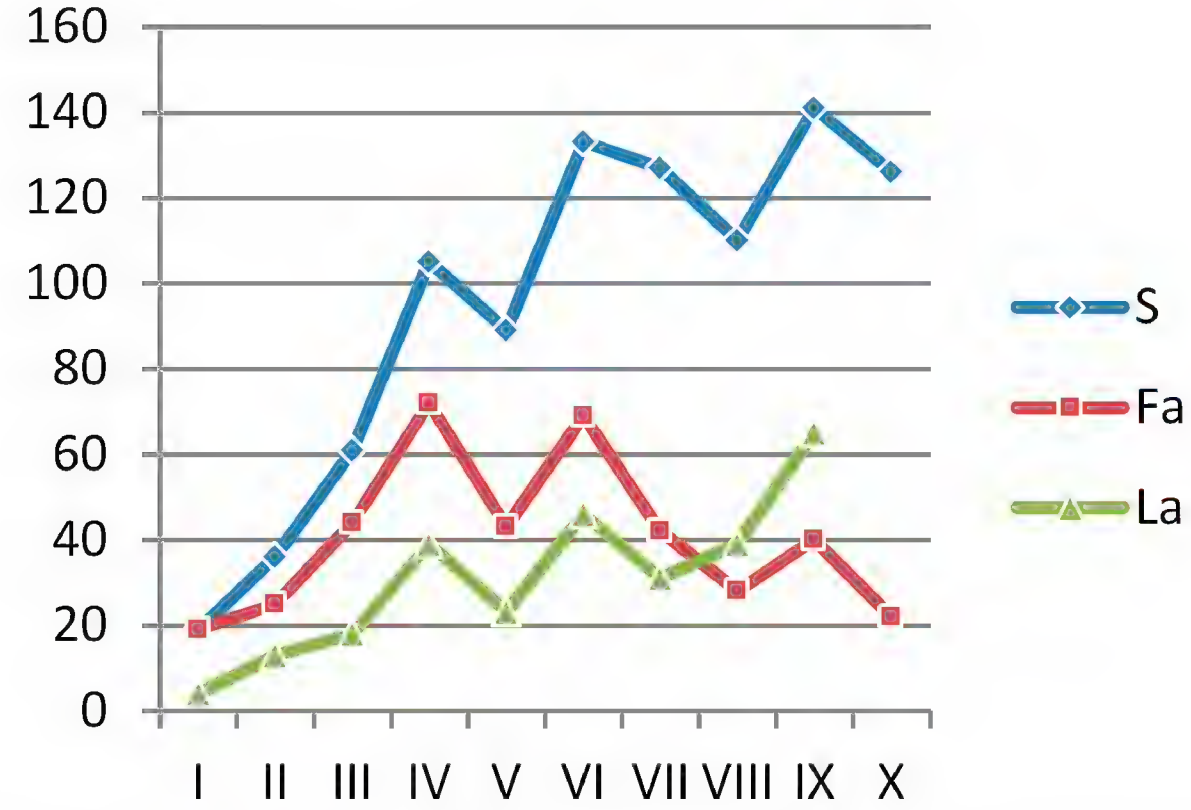


Figure 10. Summary of taxa dynamics across the study chronosequence. S – total number of taxa per zone; Fa and La – number of first and last appearances of taxa per zone.

turbance, as there is no grazing by domestic animals. In the study profile, ants have already been observed after seven years in the reedgrass meadow (Plot III). They were quite abundant at the next, shrub stage (Plot IV) and regularly occurred later. Yet the diversity of most groups of arthropods has constantly increased in spite of their presence (Figs 4–6).

In summary, the succession of all study groups of invertebrates along the paraglacial chronosequence in the relatively warm conditions of the Central Caucasus (Tsey Gorge) appears to be well-structured and directional, this being expressed through a gradual change of communities forming four successive clusters. All multi-species groups, with the only exception of the general pool of Testacea, both dead and live cells combined, demonstrate a well-defined and significant species turnover, the intensity of which is slightly decreased at the last forest stages of succession. The contribution of endemic high-montane specialized species is the highest during the earliest succession stages, raising particular concerns regarding losses of highland biodiversity during the dramatic modern shrinking of Caucasian glaciers.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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